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TULANE STUDIES IN GEOLOGY AND PALEONTOLOGY

Volume 29

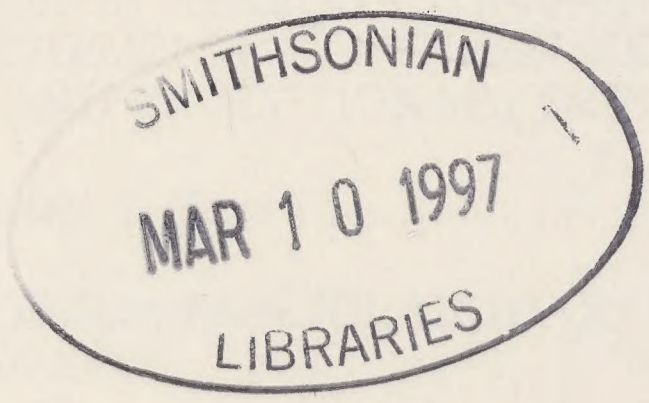
1996 - 1997

HUBERT C. SKINNER

and

EMILY H. VOKES

Editors



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TULANE STUDIES IN GEOLOGY AND PALEONTOLOGY

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PRELIMINARY DESCRIPTIONS OF 25 NEW DECAPOD CRUSTACEANS FROM THE MIDDLE EOCENE OF THE CAROLINAS, U.S.A.

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I. ABSTRACT

Twenty-three genera, 14 new, representing 12 families and comprising 25 new species of decapod crustaceans, are described from the middle Eocene Castle Hayne and Santee limestones of North and South Carolina. Of the nine existing genera, members of five, *"Paguristes," Cyrtorhina, Lophoranina, Calappilia,* and *Titanocarcinus,* had been reported previously from the Americas. The new taxa are: *"Paguristes wheeleri"* (Diogenidae); *Albunea hahnae,* the first American fossil species of the genus (Albuneidae); *Ameridromia,* type species *A. hyneorum,* and *Dromidia bedetteae,* the first fossil record for the latter genus (Dromiidae); *Prohomola katunai,* the first record of the genus outside of Japan (Homolidae); *Cyrtorhina fusseli,* the first named American species of this genus, *Lophoranina raynorae,* and *L. rossi* (Raninidae); *Titanodorippe,* type species *T. eocenica,* the largest known member of the Dorippinae (Dorippidae); *Calappilia sitzi, Eriosachila,* type species *E. petiti, Matutites,* type species *M. anthonyae,* and *Pseudohepatiscus,* type species *P. marinoi* (Calappidae); *Wilsonimaia,* type species *W. ethelae,* and *W. schneiderorum* (Majidae); *Santeecarcinus,* type species *S. harmatuki,* and *Sarahcarcinus,* type species *S. campbellorum* (Cancridae); *Acantholambrus,* type species *A. baumi* (Parthenopidae); *Viacarcinus,* type species *V. druidi,* the first fossil eumedonid and the first fossil or Recent eumedonid to be recorded from the Americas (Eumedonidae); *Eocarpilius,* type species *E. carolinensis, Eohalimede,* type species *E. walleri, Laevicarcinus dockeryi,* the first record for the genus outside of Hungary and the first American species of the genus, *Santeella,* type species *S. lillyae, Santeexanthus,* type species *S. wardi,* and *Titanocarcinus purdyi* (Xanthidae). The assemblage, as a whole, has greater affinities with the faunas of the Eocene of Hungary, Italy, and Spain than with known American Eocene faunas.

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II. INTRODUCTION

On May 25, 1972, Druid Wilson, then of the Paleontology and Stratigraphy Branch, U.S. Geological Survey, and his assistants Barbara Bedette and the senior author, visited the Superior Stone Quarry (presently the M.M. Berkeley Quarry), Berkeley County, South Carolina, to study and collect from the rich fossil deposits known to occur there. Later that same year, D. Wilson handed W. Blow a very small crab that he had found in a sediment sample from the middle Eocene Santee Limestone that had been collected during their trip. This crab, *Viacarcinus druidi,* a new genus and species, became the catalyst for the more than two decades of the authors' field work and research that followed on the Eocene decapods of the Carolinas.

During that time, with the addition of each new taxon, it became clear that this was not only one of the most diverse Eocene decapod assemblages known, but that in North America, it was unique to the Carolinas. Only five genera of this assemblage, *"Paguristes," Lophoranina, Calappilia, Eriosachila,* and *Titanocarcinus,* and no species, are found elsewhere in the Americas. In time, the affinities of this assemblage would prove to be closer to those found in the Eocene deposits of Spain, Hungary, and Italy rather than to those of other American Eocene deposits.

Our study of this assemblage has grown far beyond initial expectations, thereby delaying the publication of our planned monograph. The following three factors have contributed to our decision to prepare this preliminary account of the new taxa found to date. Firstly, only two, fairly recent, preliminary reports have dealt with the fossil decapods of the Carolinas since Rathbun's 1935 report on the fossil Crustacea of the Atlantic and Gulf Coastal Plain, and most of the identifications given in both of these reports are incorrect. Secondly, much new information on European Eocene decapods has come to light in recent years through the work of L. Via Boada in Spain, J.S.H. Collins in England, Pal Müller in Hungary, and Claudio Beschin and his colleagues in Italy. Their work, like that of some earlier European workers, though very relevant to Carolinian Eocene decapods, is, for the most part, like Rathbun (1935), out of print and/or not available in most American libraries. And finally, during the past 10 years, fossil collecting has become increasingly popular, and thousands of people have joined local fossil clubs nationwide. Fossil clubs in the mid-Atlantic states are particularly active, and the scientific value of their work would be much enhanced by provision of accurate fossil identification guides.

This preliminary report is, therefore, intended to: correct the misidentifications of Carolinian Eocene decapods already in the literature; bring to light this diverse and very interesting assemblage; and satisfy the need, in part, of the amateur collector or student of paleontology by serving as a basic, interim guide to the Carolinian Eocene decapods.

The diagnoses given below will differentiate the new genera from other genera in the same family and will distinguish the new species from all other species in their respective genera.

Repositories: Primary types are deposited in the National Museum of Natural History, Smithsonian Institution, Washington, D.C. Some paratypes, where indicated, are deposited in the Virginia Museum of Natural History, Martinsville, Virginia.

Abbreviations:

M.M., quarries owned and operated by Martin Marietta Aggregates

NMNH, National Museum of Natural History, Smithsonian Institution

P & S, the former Paleontology and Stratigraphy Branch, USGS

USGS, the U.S. Geological Survey (when used with a number indicates a locality; see locality register at end of paper)

USNM, abbreviation for catalogue numbers of the former U.S. National Museum, now the National Museum of Natural History

VMNH, Virginia Museum of Natural History

Measurements: Unless otherwise stated, all specimens are represented by the dorsal aspect of the carapace. The margins of many specimens are broken, eroded, or incomplete as indicated in a number of our figures. Measurements, therefore, represent the overall dimensions of the specimen in hand, complete or fragmentary.

Measurements are expressed in millimeters as follows: cl, carapace length, maximum longitudinal measurement; cw, carapace width, maximum transverse measurement; prl, propodus length, length of palm or combined length of palm and fixed finger; prh, propodus height; prt, propodus thickness; l, length, overall; w, width, overall.

Stratigraphic assignment: With the exception of only one specimen, the paratype of *Viacarcinus druidi,* USNM 484560, all specimens described in this paper were collected as spoil or float from their respective North and South Carolina localities. Stratigraphic assignment of these specimens, therefore, is based on the matrix associated with each specimen. All specimens have been determined to have been derived from either the middle Eocene Castle Hayne or Santee limestones. These assignments are given with each of the following species accounts.

III. ACKNOWLEDGMENTS

Many people have contributed their specimens, field, library, or other assistance to the authors in the preparation of this manuscript. Most of this assistance has been acknowledged throughout the text where appropriate. Among those cited in the text, we especially thank Druid Wilson, Gerald R. Baum, and Lauck W. Ward for their valuable insights on Carolinian Eocene stratigraphy and for opening up their respective collections to us. We are particularly grateful for the support of Thomas R. Waller, without which this project could not have been completed. Numerous discussions with Francis M. Hueber have greatly enhanced the quality of this paper. We are also particularly grateful to William O. Ross, Peter J. Harmatuk, and Judith R. Schneider for providing many of the specimens cited in this paper. This paper would not have been possible without the help of the many quarry owners and operators who have graciously allowed the authors and numerous others to collect in their quarries. In this regard we thank Martin Mariettta Aggregates, of North and South Carolina, and the Billy B. Fussel Company, Inc., Rose Hill, North Carolina.

IV. SYSTEMATIC PALEONTOLOGY

Family DIOGENIDAE Ortmann, 1892

"PAGURISTES" WHEELERI, n. sp.
Plate 1, Figure 1

Diagnosis: Specimens of right and left propodi where of equal size nearly identical in terms of proportions and ornamentation, length of each about 1 1/2 times their width. Dorsal surface of each covered with large tubercles, ventral surface of each very inflated and covered with tubercles below prominent row of much larger tubercles arranged in shape of inverted Y. Dorsomesial border of palm with double row of very large tubercles along margin. Dorsolateral border of propodus with about 12 subquadrate, faintly bilobed teeth, forming carinate margin.

Etymology: This species is named for the late Walter H. Wheeler, in recognition of his contribution to the geology and paleontology of North Carolina, through his own research efforts and those of a number of students whose interest in Carolinian paleontology was stimulated by him during his tenure as a professor of geology at the University of North Carolina, Chapel Hill.

Holotype: Left propodus (USNM 484527), prl 19.5 mm, prh 14.7 mm, prt 8.2 mm.

Type locality: USGS 26874, Maple Hill (Lanier Pit), Pender County, North Carolina. Castle Hayne Limestone.

Paratypes: Left propodus (USNM 484528), prl 20.6 mm, prh 13.9 mm, prt covered; locality USGS 26883 M.M. Berkeley Quarry, Berkeley County, South Carolina. Left propodus (USNM 484529), prl 18.2 mm, prh 12.4 mm, prt 7.9 mm, locality USGS 26883, as above. Santee Limestone.

Right propodus (USNM 488556), prl 47.3 mm, prh 31.1 mm, prt 20.0 mm. Locality unknown.

Occurrence: Castle Hayne Limestone, North Carolina; Santee Limestone, South Carolina.

Remarks: We could find no species that might be confused with this species.

Family ALBUNEIDAE Stimpson, 1858

ALBUNEA HAHNAE, n. sp.
Plate 1, Figure 2

Diagnosis: Size small (cl 16.6 mm). Carapace obovate, slightly longer than broad, regions well-defined by distinct dorsal grooves. Anterior margin almost transverse, with deep median ocular sinus armed with small, median rostral spine. Outer angle of ocular sinus with strong spine, produced well beyond anterior outline, followed laterally by 6-7 stout spiniform teeth; outer angle of anterior margin unarmed. Postfrontal region bordered posteriorly by deep, sinuous trough extending from below outer ocular spine nearly to lateral margin. Prominent, broad, M-shaped depression situated between submedian extensions of trough and laterally-bilobed protogastric regions; surface of depression appearing braided to unaided eye. Cervical groove continuous, interconnecting with 2 posteriorly directed branchial furrows.

Etymology: This species is named for Carolyn S. Hahn, former reference librarian of the Natural History Branch, Smithsonian Institution Libraries, whose pleasant demeanor and incomparable knowledge of the library's holdings in natural history materially contributed to our research.

Holotype: (USNM 484530), cl 16.6 mm, cw 13.8 mm.

Type locality: USGS 26882, M.M. Berkeley Quarry, Berkeley County, South Carolina. Santee Limestone.

Occurrence: Santee Limestone, South Carolina.

Remarks: Of the three reported fossil species of *Albunea, A. hahnae* most closely resembles *A. cuisiana* Beschin and de Angeli, 1984 from the middle Eocene of northeastern Italy, from which it differs in having: (1) a much deeper median indentation of the postfrontal M-shaped groove; (2) a cervical groove continuous with the branchial groove; and (3) the lateral branchial margin above the *linea anomurica* appears more irregular.

This is the first American record for a fossil member of *Albunea.*

Family DROMIIDAE De Haan, 1833

AMERIDROMIA, n. gen.

Diagnosis: Size small (cw 8.7 mm). Carapace subpentagonal, strongly convex, length sube-

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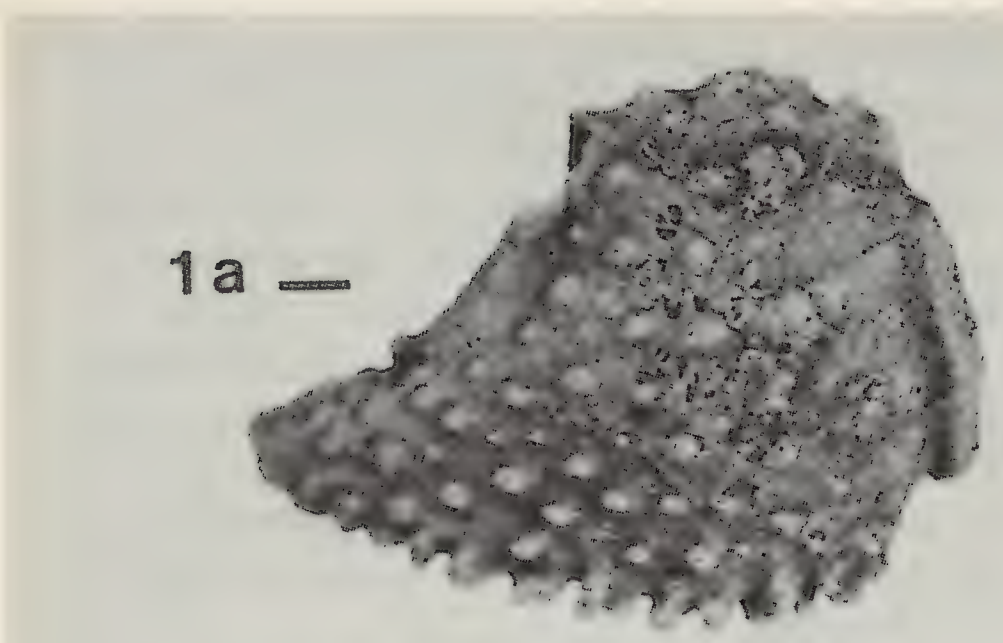
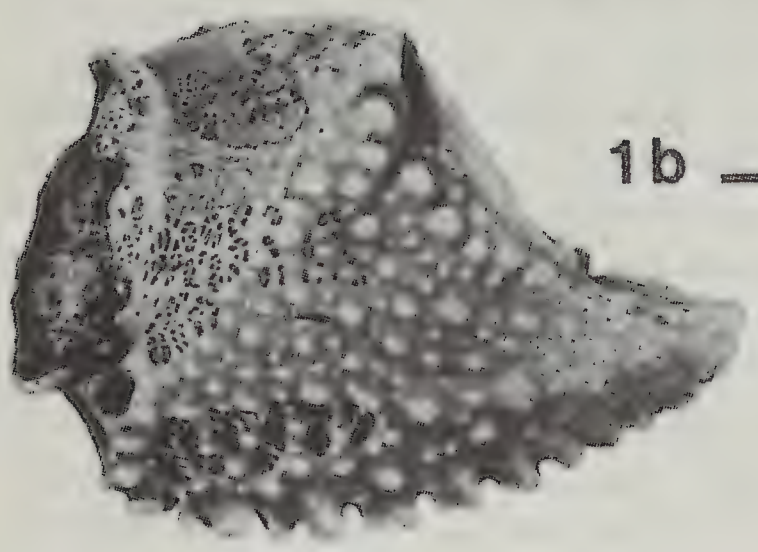
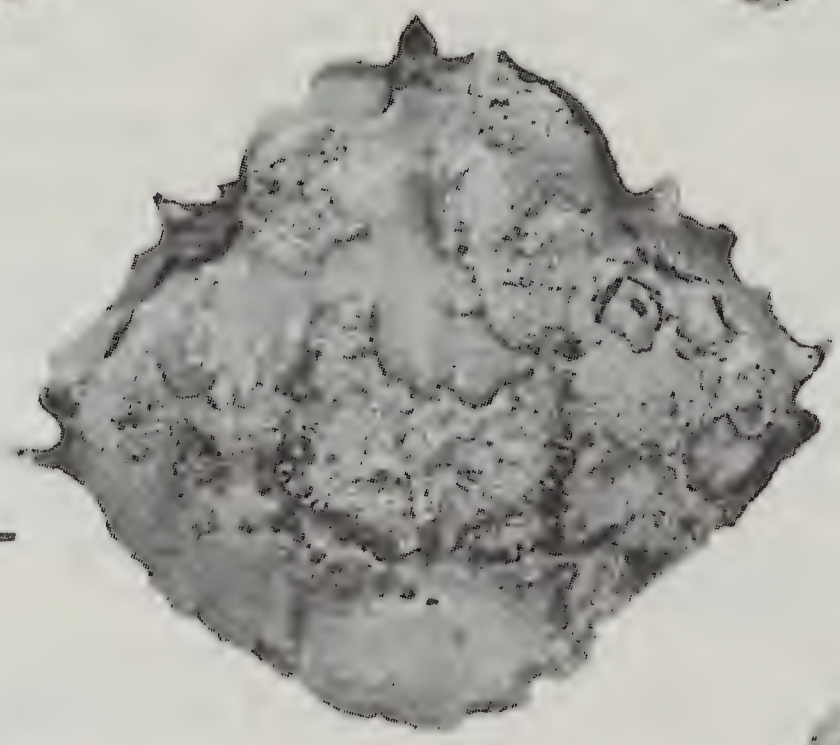
PLATE 1

Figures

1. *"Paguristes" wheeleri* Blow and Manning, n. sp.
   1a. Holotype, left propodus in dorsal view, (USNM 484527), prl 19.5 mm, prh 14.7 mm, prt 8.2 mm. Scale = 2 mm.
   1b. Holotype in ventral view. Scale = 2 mm.
   Locality: USGS 26874, Maple Hill, Pender County, North Carolina. Castle Hayne Limestone.
2. *Albunea hahnae* Blow and Manning, n. sp.
   Holotype, incomplete carapace in dorsal view, (USNM 484530), cl 16.6 mm, cw 13.8 mm. Scale = 2 mm.
   Locality: USGS 26882, Berkeley County, South Carolina. Santee Limestone.
3. *Ameridromia hyneorum* Blow and Manning, n. gen. and sp.
   Holotype, incomplete internal mold of carapace in dorsal view (truncated posteriorly along branchial groove and posterior margin of cardiac region), (USNM 484532), cl 7.6 mm, cw 8.7 mm. Scale = 2 mm.
   Locality: USGS 26883, Berkeley County, South Carolina. Santee Limestone.
4. *Dromidia bedetteae* Blow and Manning, n. sp.
   Holotype, right half of carapace in dorsal view, (USNM 484531), cl 13.2 mm, cw 8.6 mm. Scale = 2 mm.
   Locality: USGS 26883, Berkeley County, South Carolina. Santee Limestone.
5. *Prohomola katunai* Blow and Manning, n. sp.
   Holotype, incomplete carapace in dorsal view (truncated anteriorly and terminating laterally along *linea homolica*), (USNM 484533), cl 27.9 mm, cw 21.5 mm. Scale = 2 mm.
   Locality: USGS 26882, Berkeley County, South Carolina. Santee Limestone.







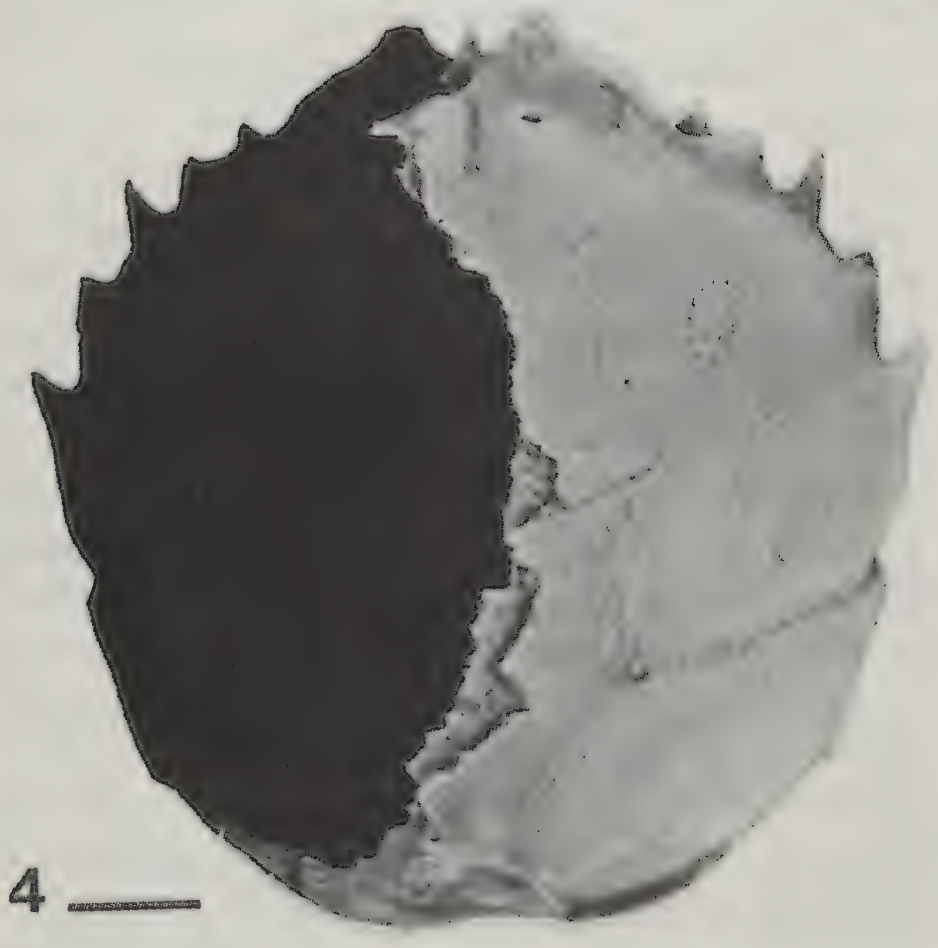


PLATE 1

qual to width. Regions moderately well-defined anteriorly. Surface sparsely pustulose and/or tuberculate anteriorly. Front tridentate, rostrum strongly projecting. Inner orbital lobe continuous with lateral frontal lobe, produced into broad, convex eave. Outer orbital lobe very strong. Anterolateral margins nearly vertical, strongly convergent anteriorly. Anterolateral teeth 4, conical in shape, first beginning well below and behind outer orbital lobe, third and fourth closely set, nearly paired.

Type species: Ameridromia hyneorum, n. sp., by present designation and monotypy.

Etymology: The name combines America and the generic name *Dromia.* Gender feminine.

Remarks: The characters of *Ameridromia* exclude this new genus from all known genera in the family Dromiidae (see McLay, 1993). These same features do, however, suggest much stronger affinities with Recent, more advanced members of this diverse family than with extinct forms.

AMERIDROMIA HYNEORUM, n. sp.
Plate 1, Figure 3

Diagnosis: As for genus.

Etymology: This species is named for Frank and Becky Hyne, of Greenville, North Carolina, in appreciation of their ongoing collecting efforts which have greatly benefited this paper and the NMNH collections.

Holotype: (USNM 484532), cl 7.6 mm, cw 8.7 mm.

Type locality: USGS 26883, M.M. Berkeley Quarry, Berkeley County, South Carolina. Santee Limestone.

Occurrence: Santee Limestone, South Carolina.

DROMIDIA BEDETTEAE, n. sp.
Plate 1, Figure 4

Diagnosis: Size small (cl 13.2 mm). Carapace strongly convex transversely, length slightly more than width, broadest at third anterolateral tooth, regions poorly defined. Fronto-orbital region about 2/3 width of carapace. Frontal region armed with 3 distinct, acute teeth. Median tooth deflexed below and not projecting beyond adjacent teeth of broadly triangular frontal lobes. Outer orbital lobe, strongly produced at external angle, but without spine. Suborbital lobe broadly triangular, strongly produced beyond orbital margin above. Lateral margin of carapace with 4 teeth, first strongest, spiniform, tip nearly reaching outer orbital angle. Second tooth broad, not spiniform like first and third nor as strong. Fourth tooth weak, set just behind branchial groove. Cardiac region with 3 minute tubercles which when connected form corners of an inverted triangle.

Etymology: This species is named for Barbara A. Bedette, formerly of the P & S Branch, USGS, in recognition of her many contributions to paleontology. In addition, Ms Bedette assisted in collecting some of the material described in this paper.

Holotype: (USNM 484531), cl 13.2 mm, cw 8.6 mm.

Type locality: USGS 26883, M.M. Berkeley Quarry, Berkeley County, South Carolina. Santee Limestone.

Occurrence: Santee Limestone, South Carolina.

Remarks: Dromidia bedetteae appears most closely allied to the Recent crab, *D. antillensis* Stimpson, 1859, from which it can be immediately distinguished by: (1) its strong, elongate first and third anterolateral teeth, the first of which extends almost to the tip of the outer orbital angle; and (2) the outer angle of the frontal lobe of *D. bedetteae,* unlike that of *D. antillensis,* is rounded and lacks a spine.

Dromidia bedetteae is the first recorded fossil member of this genus.

Family HOMOLIDAE White, 1847

PROHOMOLA KATUNAI, n. sp.
Plate 1, Figure 5

Diagnosis: Carapace distinctly longer than broad, regions well-defined. Dorsal surface anteriorly elevated, prominences coarsely tuberculate; posterior surface flattened, more densely tuberculate. Protogastric region divided into 3 distinct lobes; anterolateral lobe with very prominent, obliquely directed, acute spine. Mesogastric region basally divided into 3 lobes; medial lobe most prominent, longitudinally subovate, strongly inflated, coarsely granulate. Anterior process of mesogastric region narrow. Cardiac region longitudinally subobovate, with shallow, longitudinal depression, surface with fine tubercles.

Etymology: This species is named for Michael P. Katuna, Professor and Chairman of Geology, College of Charleston, Charleston, South Carolina for his contribution to South Carolina geology and paleontology through his teaching

and for his help in collecting a number of species described herein.

Holotype: (USNM 484533), cl 27.9 mm, cw 21.5 mm.

Type locality: USGS 26882, M.M. Berkeley Quarry, Berkeley County, South Carolina. Santee Limestone.

Paratype: (USNM 484534), l 24.6 mm, w 12.5 mm; locality USGS 26883, same quarry as above. Santee Limestone.

Occurrence: Santee Limestone, South Carolina.

Remarks: This species resembles the type species of the genus, *P. japonica* (Yokoyama, 1911), in general facies but can immediately be separated from *P. japonica* by: (1) the presence of a strong, acute spine on the anterolateral lobe of the protogastric region; (2) larger or much coarser, though fewer, granules on the carapace surface, especially anteriorly; and (3) a much broader, more elevated, and more coarsely granulated basal circular lobe of the mesogastric region.

This is the first American record as well as the first record of this genus outside of Japan.

Family RANINIDAE De Haan, 1841

CYRTORHINA FUSSELI, n. sp.
Plate 2, Figure 1

Diagnosis: Carapace obovate, widest anteriorly, just behind third anterolateral tooth. Front tridentate, base narrow, about 1/4 carapace width. Anterolateral margin with 3 stout spinulose teeth, distance from first to second distinctly less than distance from second to third. Lateral margin behind base of third anterolateral tooth, broad, coarsely tuberculate. Postfrontal region with irregular medial row of tubercles extending from narrow, transverse field of tubercles onto base of rostrum. Posterior margin of carapace distinctly greater than 1/3 of carapace width.

Etymology: This species is named for Billy B. Fussel, of Rose Hill, North Carolina, in appreciation of his support in making his quarry available to us for collecting and for sharing with us a number of specimens that he or members of his family had discovered.

Holotype: (USNM 484544), cl 27.7 mm, cw 25.0 mm.

Type locality: USGS 26870, M.M. Castle Hayne Quarry (formerly Superior Stone Quarry), Castle Hayne, North Carolina. Castle Hayne Limestone.

Paratype: (USNM 484545), cl 29.1 mm, cw 25.3 mm. Locality USGS 26876, Billy B. Fussel Company, Inc., Quarry, Rose Hill, North Carolina. Castle Hayne Limestone.

Occurrence: Castle Hayne Limestone, North Carolina.

Remarks: Cyrtorhina fusseli appears most similar to *C. globosa* Beschin *et al.,* 1988, from the Eocene of northern Italy from which it can be separated as follows: (1) the carapace of *C. fusseli* is widest anteriorly, just behind the third or posteriormost anterolateral tooth, not posterior to midlength as in *C. globosa;* (2) the width of posterior margin of the carapace of *C. fusseli* is distinctly greater than 1/3 of the carapace width, but it is narrower, less than 1/3 of the carapace width in *C. globosa;* (3) the tubercles making up the transverse field of tubercles on the postfrontal region of *C. fusseli* appear larger, more advanced anteriorly, and have an irregular medial row of tubercles extending onto the rostrum, characters unlike those seen on the illustrations of *C. globosa.*

This is the first named record of a fossil or Recent species of *Cyrtorhina* from the Americas.

LOPHORANINA RAYNORAE, n. sp.
Plate 2, Figure 3

Diagnosis: Carapace broadly obovate, widest at anterolateral angle. Front broad, strongly biconcave, width half width of fronto-orbital region. Lateral frontal lobes strongly produced laterally into sharp, acute angle. Outer orbital lobe with strong lateral spine slightly deflected anterolaterally. Anterolateral margin with 2 flattened, subequal, hook-like spines behind outer orbital lobe. Dorsal surface ornamented with numerous, short, interrupted, transverse, pectinate ridges, anastomosing irregularly. Ridge elements exceeding 200 in number.

Etymology: This species is named for Judith A. Raynor Schneider, of Garner, North Carolina, who collected the type material and brought this unique new crab to the senior author's attention.

Holotype: (USNM 484541), cl 43.5 mm, cw 37.2 mm.

Type locality: USGS 26870, M.M. Castle Hayne Quarry, Castle Hayne, North Carolina. Castle Hayne Limestone.

Paratypes: (USNM 484542), cl 28.3 mm, cw 24.6 mm; locality USGS 26870, as above; (USNM 484543), cl 29.7 mm, cw 23.5 mm; locality USGS 26871, same quarry as 26870, above. Castle Hayne Limestone.

Occurrence: Castle Hayne Limestone, North Carolina.

Remarks: This species can be distinguished from all other species in the genus by the presence of two narrow, hooked, anterolateral teeth and a dorsal surface ornamented with numerous, short, interrupted, transverse, pectinate ridges, anastomosing irregularly; no ridges completely cross the carapace. Unlike the transverse ridges found in other species of *Lophoranina,* the ridge elements of *L. raynorae* appear fragmented and are numerous, exceeding 200 in number; some appear castellate and/or capillate.

The two species of *Lophoranina* named here double the number of recognized American species of the genus.

LOPHORANINA ROSSI, n. sp.
Plate 2, Figure 4

Diagnosis: Carapace broadly obovate, widest behind anterolateral angle. Anterolateral margin produced anteriorly into 2 broad, blade-like teeth separated from outer orbital lobe by 2 small teeth. Dorsal surface ornamented with numerous transverse, pectinate ridges, numbering 20 to 25 on midline. Ridges widely spaced and more or less complete anteriorly, closely spaced and anastomosing posteriorly. Pectinate ridges straightening anteriorly. Inferior margin of palm of right chela produced into 4 large, blade-like, subparallel teeth. Superior, inner, distal angle of articulated carpus armed with very long, narrow, inwardly directed spine.

Etymology: This species is named for William O. Ross, formerly of the P & S Branch, USGS, in recognition of his many contributions to paleontology and with particular appreciation for collecting much of the material described in this paper.

Holotype: (USNM 484535), cl 35.7 mm, cw 31.5 mm; prl 17.7 mm, prh 12.5 mm.

Type locality: USGS 26878, M.M. Georgetown Quarry, Georgetown County, South Carolina. Santee Limestone.

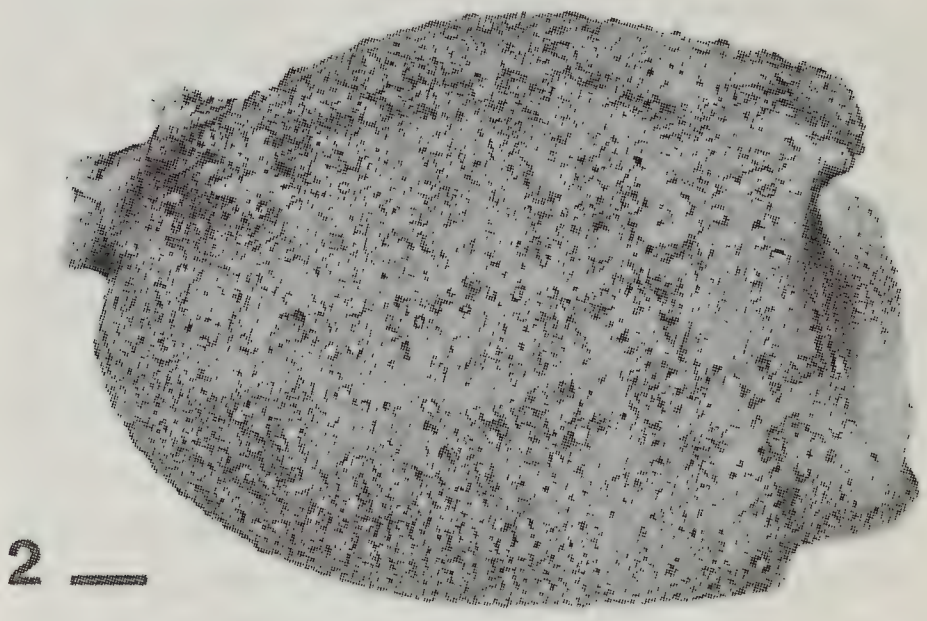
Paratypes: (USNM 484536), cl 47.1 mm, cw 34.2 mm; (USNM 484537), cl 44.2 mm, cw 38.9 mm; (USNM 484540), cl 23.8 mm, cw 36.0 mm; (USNM 484536-484537 & 484540), locality USGS 26878, as above; (USNM 484538), cl 35.1 mm, cw 28.4 mm; (USNM 484539), cl 44.2 mm, cw 36.9 mm; (USNM 484538-484539), locality USGS 26880, same quarry as locality USGS 26878, above. Santee Limestone. In addition, three paratypes have been deposited in the VMNH.

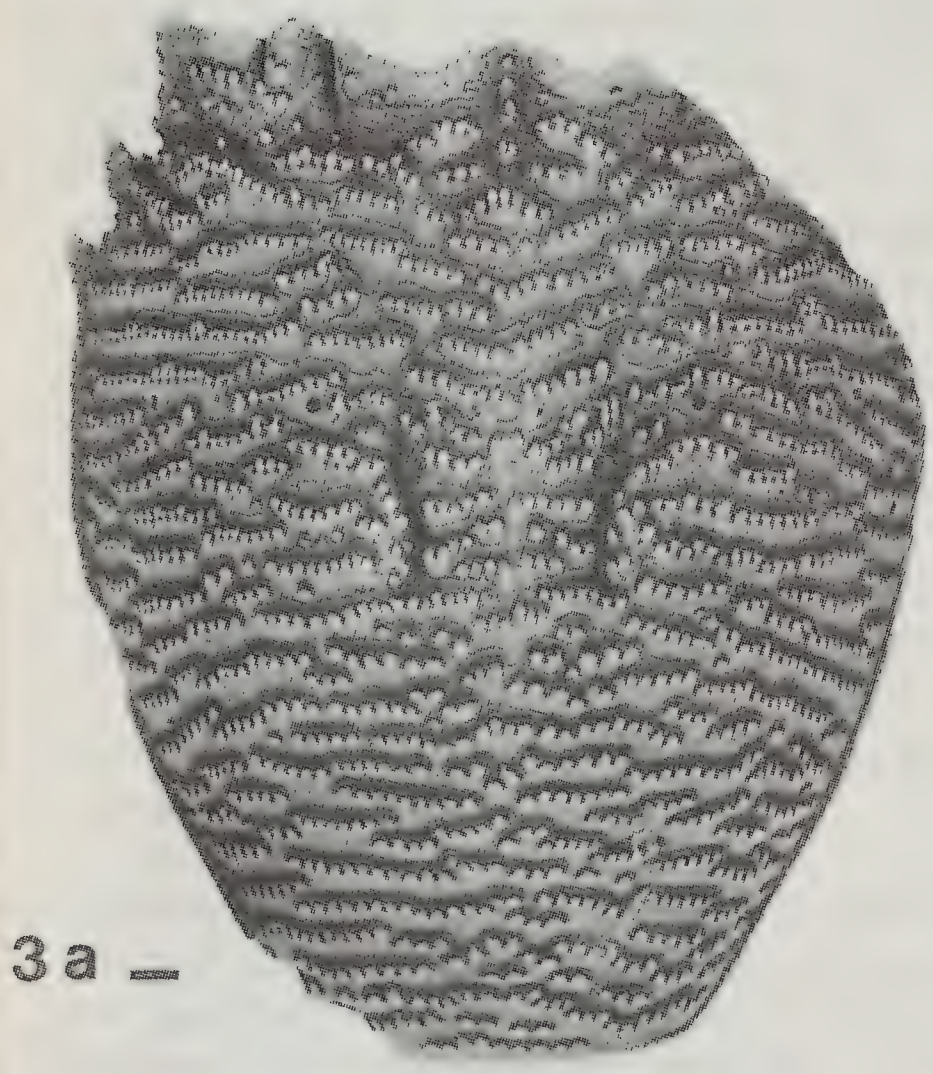
Occurrence: Santee Limestone, South Carolina.

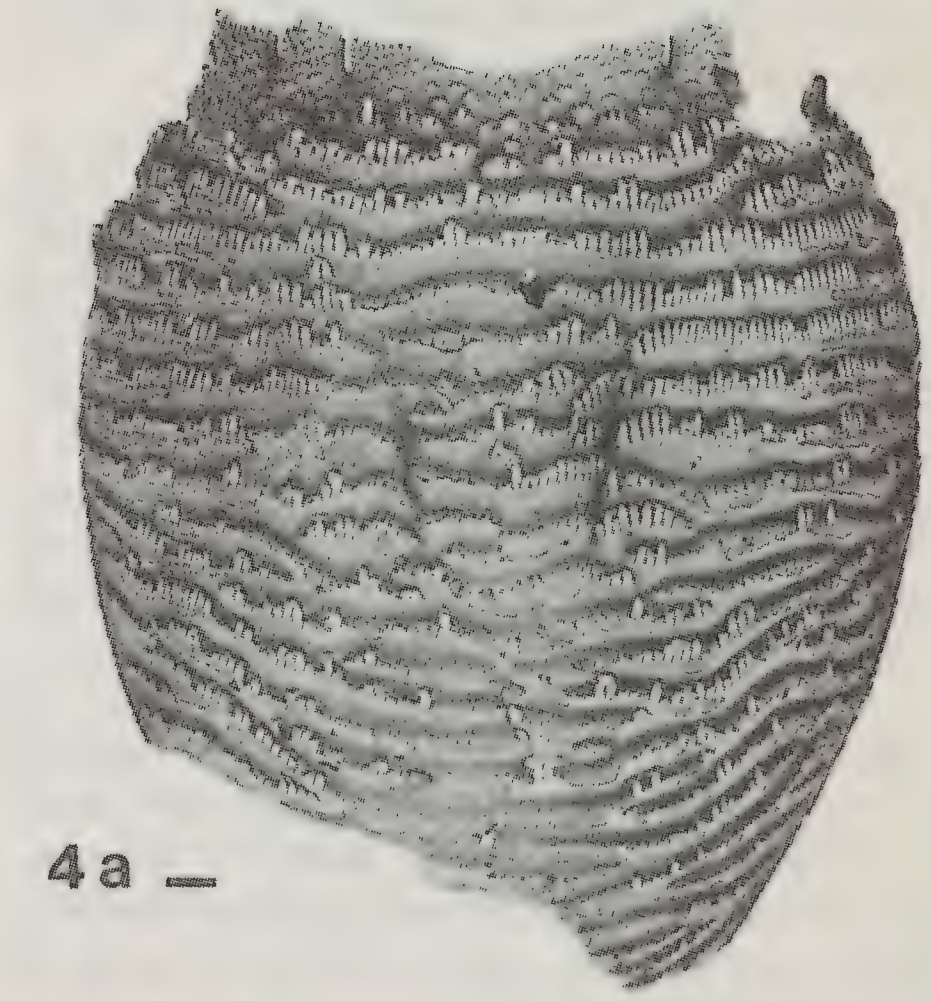
PLATE 2

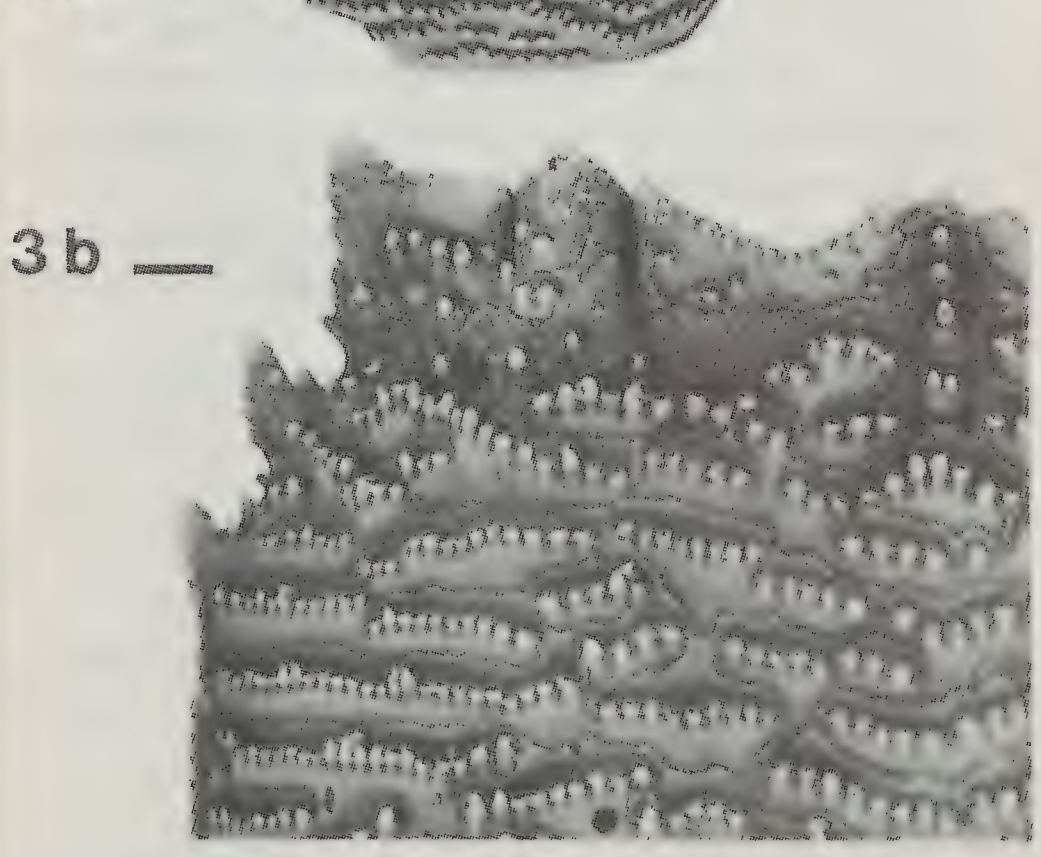
Figures

1. *Cyrtorhina fusseli* Blow and Manning, n. sp.
   Holotype, incomplete carapace in dorsal view (fronto-orbital region lacking), (USNM 484544), cl 27.7 mm, cw 25.0 mm. Scale = 2 mm.
   Locality: USGS 26870, Castle Hayne, North Carolina. Castle Hayne Limestone.
2. *Titanodorippe eocenica* Blow and Manning, n. gen. and sp.
   Holotype, incomplete right propodus in outer view, (fixed finger and dactylus lacking), (USNM 488557), prl 46.5 mm, prh 31.9 mm, prt 22.0. Scale = 4 mm.
   Locality: USGS 26884, Berkeley County, South Carolina. Santee Limestone.
3. *Lophoranina raynorae* Blow and Manning, n. sp.
   3a. Holotype, incomplete carapace in dorsal view (rostrum incomplete, right orbit and right anterolateral margin lacking), (USNM 484541), cl 43.5 mm, cw 37.2 mm. Scale = 2 mm.
   3b. Holotype, close-up of left fronto-orbital and anterolateral margins. Scale = 2 mm.
   Locality: USGS 26870, Castle Hayne, North Carolina. Castle Hayne Limestone.
4. *Lophoranina rossi* Blow and Manning, n. sp.
   4a. Holotype, incomplete carapace in dorsal view (rostrum lacking and posterior margin incomplete), (USNM 484535), cl 35.7 mm, cw 31.5 mm. Scale = 2 mm.
   4b. Holotype, close-up of left fronto-orbital and anterolateral margins. Scale = 2 mm.
   Locality: USGS 26878, Georgetown County, South Carolina. Santee Limestone.









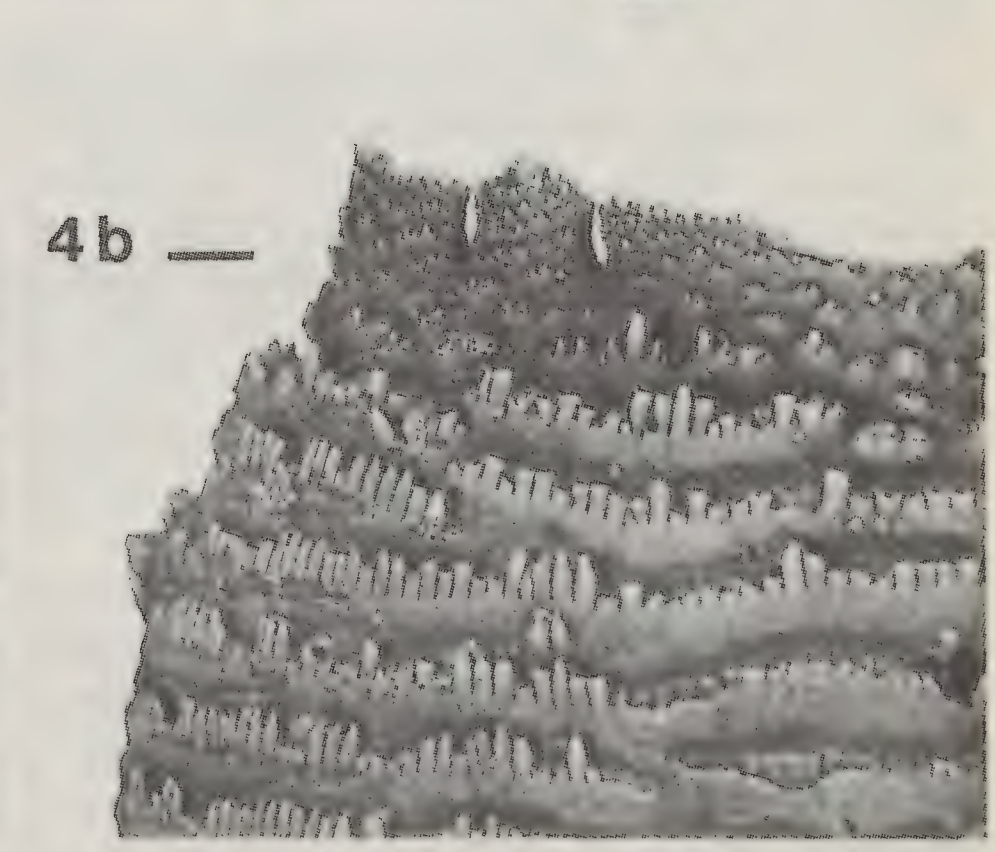


PLATE 2

Remarks: This species most closely resembles *L. laevifrons* (Bittner, 1875) from the Eocene of Italy, from which it can be easily separated by its: (1) broader, more ornate post fronto-orbital surface; (2) less interrupted anterior dorsal ridges; and (3) two broad, flattened, ear-like anterolateral teeth.

Lophoranina rossi can be readily separated from *L. straeleni* Via Boada, 1959, from the Eocene of Spain, with which it was tentatively identified by Bishop and Whitmore (1986, p. 299), by its: (1) narrower post fronto-orbital dorsal surface; (2) straight, not concave, less interrupted anterior ridges; and (3) two broader, more flattened, ear-like anterolateral teeth.

Family DORIPPIDAE de Haan, 1841
Subfamily DORIPPINAE de Haan, 1841

TITANODORIPPE, n. gen.

Diagnosis: Size very large (prl 46.5 mm) for dorippids, much larger than any Recent genus of the Dorippidae.

Type species: Titanodorippe eocenica, n. sp., by present designation and monotypy.

Etymology: From the Greek, *Titan,* gigantic or colossal, alluding to the apparent large size of the type species, in combination with the generic name *Dorippe.* Gender feminine.

Remarks: The single palm of an adult male agrees in all respects except size with the larger palm of adult males of Recent members of the genera *Dorippe* Weber, 1795, and *Medorippe* Manning and Holthuis, 1981.

The largest male of a *Dorippe* reported by Holthuis and Manning (1990) has a carapace width of 43 mm, much smaller than the projected carapace width of 62 mm based on a propodus height of 31.9 mm in *T. eocenica,* assuming a 2:1 ratio of carapace width/propodus height. We have found no intact carapace, legs, or fragments of a dorippid this large in our collections.

In the Recent Dorippinae, the smaller male chela and the female chelae all have a single longitudinal groove in the upper third of the outer surface. Although their palms are typically smooth and shiny, lacking tubercles or spines, both palms in the male may be covered with granules, as in *D. irrorata* Manning and Holthuis, 1986 (see Holthuis and Manning, 1990, p. 17; granules not shown fig. 4d)..

This is largest known member of the Dorippinae and the first described member of the subfamily from the Americas.

TITANODORIPPE EOCENICA, n. sp.
Plate 2, Figure 2

Diagnosis: Palm with inner and outer surfaces inflated, completely covered with granules. Palm highest in middle, height about half maximum outer length of palm, about 2/3 dorsal length. Distal edge of palm with more than 25 distinct denticles.

Etymology: The specific name is based on the Eocene stratigraphic occurrence of the type species.

Holotype: (USNM 488557), prl 46.5 mm, prh 31.9 mm, prt 22.0 mm.

Type locality: USGS 26884, M.M. Berkeley Quarry, Berkeley County, South Carolina. Santee Limestone.

Occurrence: Santee Limestone, South Carolina.

Remarks: The size of the propodus of this species distinguishes it from all known dorippids.

Family CALAPPIDAE de Haan, 1833
Subfamily CALAPPINAE de Haan, 1833

CALAPPILIA SITZI, n. sp.
Plate 3, Figure 1

Diagnosis: Carapace subpentagonal, strongly convex, length slightly less than width, broadest at midlength. Anterolateral margin armed with about 11 small to minute teeth, acute, unequal, alternating in size. Posterolateral margin greatly expanded, winglike, armed with 5 to 6 medium to moderately large, acute, very coarsely granulated teeth. Posterior margin coarsely granulate, trilobate. Protogastric region with 1 central protuberance; mesogastric protuberance elongate, greatly elevated; urogastric region with 1 central protuberance; cardiac region with 1 strong central protuberance; hepatic region with 2 to 4 protuberances; branchial region with 3 very strong protuberances adjacent and subparallel to gastrocardiac groove, bordered laterally by a second row of 8 slightly smaller protuberances.

Etymology: This species is named for Thomas O. Sitz, Professor of Biochemistry, Virginia Tech, Blacksburg, Virginia, in appreciation for

his many years of field support and encouragement of the senior author, and in recognition of his own extensive contribution to science and education.

Holotype: (USNM 484546), cl 15.9 mm, cw 16.6 mm.

Type locality: USGS 26874, Lanier Pit, Maple Hill, Pender County, North Carolina. Castle Hayne Limestone.

Paratypes: (USNM 484547) cl 11.7 mm, cw 12.1 mm; (USNM 484548) cl 12.3 mm, cw 14.1 mm; (USNM 484549) cl 17.4 mm, cw 16.5 mm; (USNM 484550) cl 12.4 mm, cw 13.5 mm; (484547-484550) locality USGS 26874, as above. Castle Hayne Limestone.

Occurrence: Castle Hayne Limestone, North Carolina.

Remarks: Calappilia sitzi was confused with *C. brooksi* Ross and Scolaro, 1964, from the upper Eocene of Florida by Bishop and Whitmore (1986, p. 300, fig. 3I).

Calappilia sitzi differs from *C. brooksi* in having: (1) a more subpentagonal carapace outline; (2) broader posterolateral teeth; (3) weaker, less pronounced anterolateral teeth; (4) a greatly elevated, elongate mesogastric protuberance; (5) a single, medially-placed urogastric tubercle; and (6) the presence of large protuberances posteriorly.

Calappilia sitzi is similar in outline and in the distribution of its largest protuberances to *C. diglypta* Stenzel, 1934, from the middle Eocene of Texas. It can, however, be immediately distinguished from *C. diglypta* by: (1) its trilobate posterior margin as opposed to the condition in *C. diglypta* in which the posterior margin is produced into three closely spaced spines; and (2) its 20 or more branchial protuberances compared to only 12 in *C. diglypta.*

Subfamily MATUTINAE Alcock, 1896

ERIOSACHILA, n. gen.

Diagnosis: Carapace sub-octagonal, length slightly less than width, broadest at second or third anterolateral tooth; dorsal surface very uneven, regions well defined, surface with 8 large protuberances; those of protogastric and mesogastric regions forming raised platform. Front weakly projecting, bilobed, with deep, open, median incision, width about 1/4 carapace width; lobes truncate, divergent, anterior margins denticulate. Orbit small, subcircular, marginal. Orbit bordered below and laterally by narrow, flattened, broadly triangular, vertical, suborbital flank. Anterolateral margin divided into 4 distinct, lobe-like teeth; teeth separated by closed incisions. Posterolateral margin with 3 teeth. Posterior margin very narrow, width equal to or slightly less than width of front.

Type species: Eriosachila petiti, n. sp., by present designation.

Etymology: The name is formed by adding the Greek, *eri,* early, to the generic name *Osachila.* Gender feminine.

Included species: Eriosachila rathbunae (Maury, 1930), n. comb., Eocene, Venezuela; *Eriosachila terryi* (Rathbun, 1937), n. comb., upper Eocene, Panama; and *Eriosachila petiti,* n. sp., middle Eocene, South Carolina, USA.

Remarks: In carapace outline; number and position of lateral teeth; the presence of eight large dorsal protuberances, of which the paired mesobranchial are weakest; and the greatly elevated, protogastric, mesogastric and epibranchial regions, *Eriosachila* appears most closely allied to *Osachila* Stimpson, 1871, s.s., and other related Western Atlantic species. It differs from *Osachila*, however, in having an anteriorly broader, more truncate, much less projecting denticulate front. In addition, the frontal lobes of *Eriosachila,* unlike *Osachila,* are separated by a relatively deep, open incision and the anterior margins of the lobes are weakly divergent. In contrast, the front of *Osachila* is strongly projecting, relatively narrow anteriorly, and each lobe is distinctly rounded or acute anteriorly.

Some members of *Eriosachila* have been confused with species of *Hepatiscus* Bittner, 1875, from which they can be readily separated. In *Eriosachila,* as in *Osachila* s.s., the anterolateral margins are divided by closed incisions into four distinct lobe-like teeth, and the posterolateral margins into three teeth. In contrast, the lateral margins of *Hepatiscus* s.s., as described and figured in Bittner's original account of its type species, are wholly entire ("Der Seitenrand ist vollstandig ganzrandig") (Bittner, 1875, p. 75-76), continuous, not divided into teeth or lobes.

ERIOSACHILA PETITI, n. sp.
Plate 3, Figure 2

Diagnosis: As for genus except: dorsal protuberances relatively low, very rounded, epibranchial protuberance most prominent, distinctly laterally placed. First posterolateral tooth weak; second very strong; third largest, most prominent of all lateral teeth.

Etymology: This species is named for Richard E. Petit, malacologist, of North Myrtle Beach, South Carolina, in recognition of his contribution to Atlantic Coastal Plain paleontology and in appreciation for his years of support of the senior author's research.

Holotype: (USNM 484551), cl 8.7 mm, cw 9.7 mm.

Type locality: USGS 26878, M.M. Georgetown Quarry, Georgetown County, South Carolina. Santee Limestone.

Paratypes: (USNM 484552), cl 13.2 mm, cw 14.2 mm; locality USGS 26878, as above; (USNM 484553), cl 17.5 mm, cw 20.4 mm; locality USGS 26881, same quarry as above. Santee Limestone.

Occurrence: Santee Limestone, South Carolina.

Remarks: Eriosachila petiti differs from *E. rathbunae* in having lower, more rounded dorsal protuberances of which, unlike those of *E. rathbunae,* the epibranchial protuberance is most prominent and more laterally placed. In addition *E. petiti* differs from *E. rathbunae* in having a much weaker mesobranchial protuberance, and the third posterolateral tooth of *E. petiti* is much stronger than the same, though rudimentary, tooth in *E. rathbunae. Eriosachila petiti* can be readily separated from *E. terryi* by its more rounded and more laterally placed epibranchial protuberance. Also, in *E. petiti,* the first posterolateral tooth is weakest and third strongest and most prominent in contrast to those in *E. terryi* where the first posterolateral tooth is strongest and third weakest.

MATUTITES, n. gen.

Diagnosis: Carapace broadly obovate, length slightly less than width, broadest at third anterolateral denticle; dorsal surface weakly elevated, uneven, regions defined by 8 large pro-

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PLATE 3

Figures

1. *Calappilia sitzi* Blow and Manning, n. sp.
   Holotype, weathered carapace in dorsal view, (USNM 484546), cl 15.9 mm, cw 16.6 mm. Scale = 2 mm.
   Locality: USGS 26874, Maple Hill, Pender County, North Carolina. Castle Hayne Limestone.
2. *Eriosachila petiti* Blow and Manning, n. gen. and sp.
   Holotype, internal mold of carapace in dorsal view (surface with remnants of weathered cuticle), (USNM 484551), cl 8.7 mm, cw 9.7 mm. Scale = 2 mm.
   Locality: USGS 26878, Georgetown County, South Carolina. Santee Limestone.
3. *Matutites anthonyae* Blow and Manning, n. gen. and sp.
   Holotype, internal mold of left half of carapace in dorsal view (surface with remnants of weathered cuticle), (USNM 484554), cl 17.5 mm, cw 15.1 mm. Scale = 2 mm.
   Locality: USGS 26883, Berkeley County, South Carolina. Santee Limestone.
4. *Pseudohepatiscus marinoi* Blow and Manning, n. gen. and sp.
   Holotype, carapace in dorsal view (front incomplete), (USNM 484555), cl 11.5 mm, cw 12.5 mm. Scale = 2 mm.
   Locality: USGS 26879, Georgetown County, South Carolina. Santee Limestone.
5. *Wilsonimaia ethelae* Blow and Manning, n. gen. and sp.
   5a. Holotype, weathered carapace in lateral view (rostrum truncated near base), (USNM 484561), cl 36.4 mm, cw 18.5 mm. Scale = 2 mm.
   5b. Holotype, in dorsal view. Scale = 2 mm.
   Locality: USGS 22329, Pender County, North Carolina. Castle Hayne Limestone.
6. *Wilsonimaia schneiderorum* Blow and Manning, n. gen. and sp.
   Holotype, incomplete carapace in dorsal view (truncated anteriorly just behind orbits), (USNM 484562), cl 37.3 mm, cw 24.2 mm. Scale = 2 mm.
   Locality: USGS 26872, New Hanover County, North Carolina. Castle Hayne Limestone.

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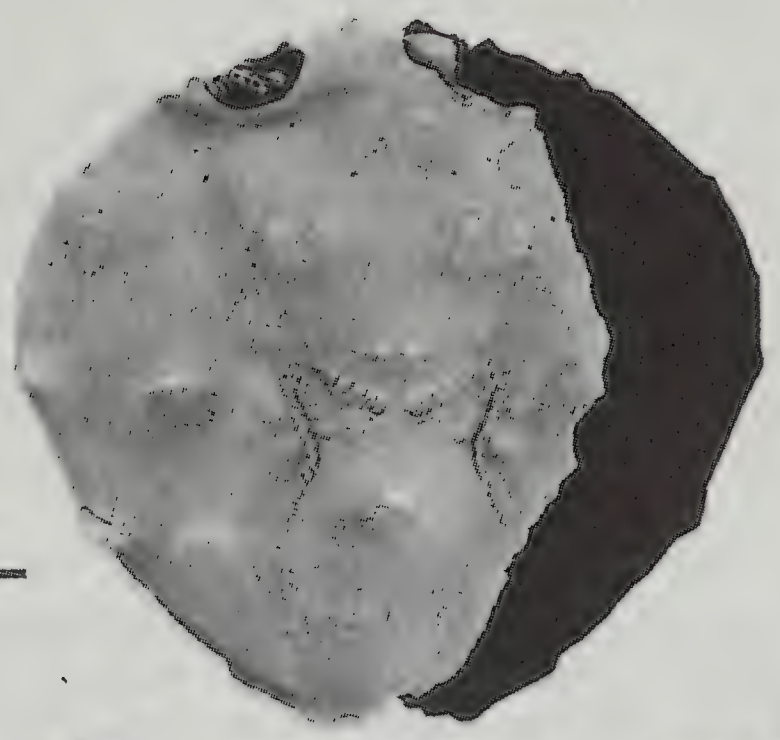
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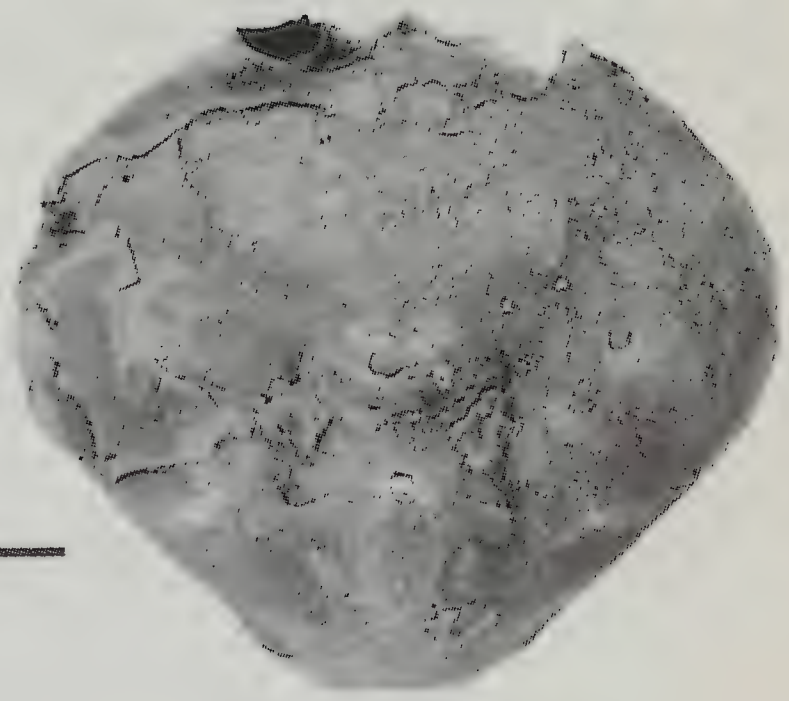
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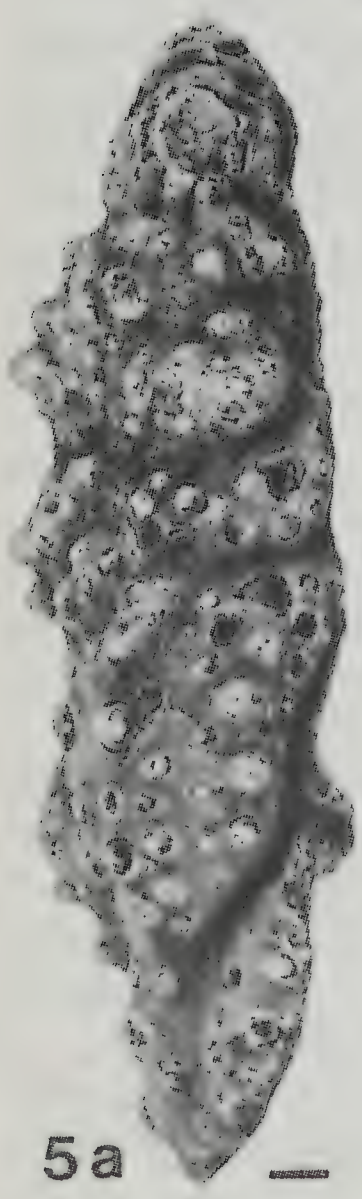
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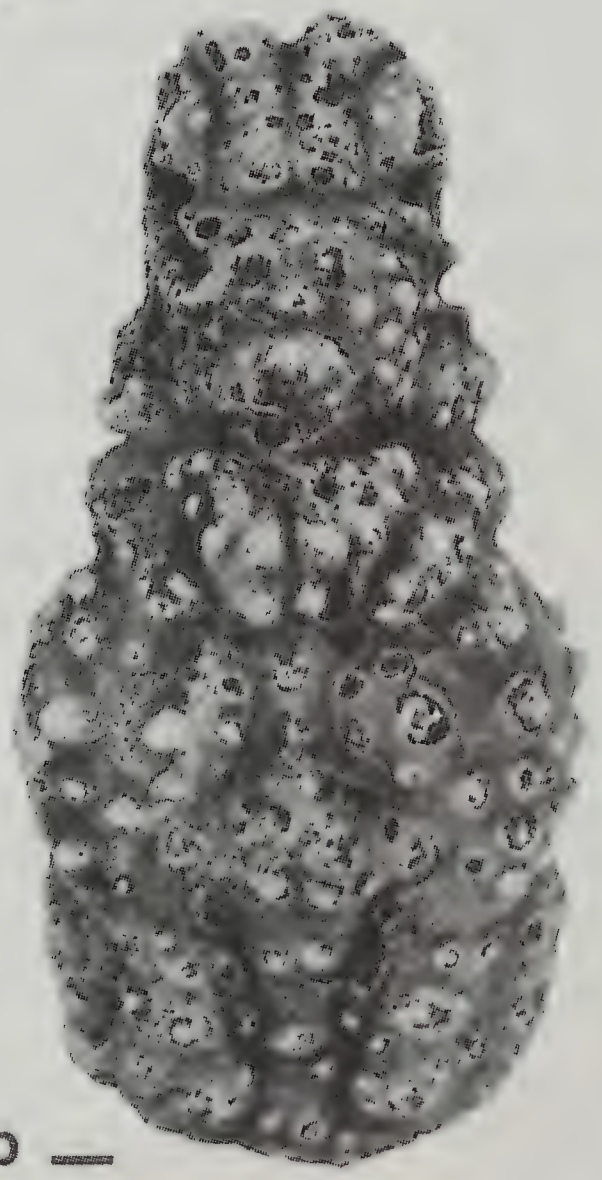
5b —

6 —

PLATE 3

tuberances. Front weakly projecting, quadridentate, with shallow median depression, width slightly less than 1/4 carapace width. Fronto-orbital width subequal to half carapace width. Orbit subcircular, marginal, produced at exorbital margin. Anterolateral margin entire, not divided into teeth or lobes by incisions, distinctly scalloped along edge in lateral view; margin with 3 denticles, third very strong, tooth-like. Anteriorly, marginal carina not reaching orbit, terminating below it. Posterolateral margins distinctly convex, strongly convergent posteriorly, armed with 1 prominent carinate lobe. Posterior margin truncate, very narrow, width subequal to front.

Type species: Matutites anthonyae, n. sp., by present designation and monotypy.

Etymology: Formed by combining the generic name *Matuta* with the ending reserved for fossil taxa, *-ites.* Gender masculine.

Remarks: In general appearance *Matutites* is reminiscent of the genus *Matuta* Weber, 1795, from which it can be readily separated by the absence of a strong spine at the anterolateral angle of the carapace (see Galil and Clark, 1994).

Matutites superficially resembles *Hepatiscus* s.s. from which it can at once be differentiated by: (1) its scalloped anterolateral margin (visible in lateral view); (2) the presence of eight dorsal protuberances, as opposed to six in *Hepatiscus;* (3) its strong tooth at the anterolateral angle; (4) the presence of a very strong, carinate posterolateral lobe; and (5) the absence of a suborbital flank like that found in *Hepatiscus, Eriosachila, Osachila, Hepatus* Latreille, 1802, and *Hepatella* Smith, 1869.

Matutites is somewhat similar to *Pseudohepatiscus,* n. gen., in carapace outline, but it differs from the latter in having: (1) convex, not straight posterolateral margins; (2) a single large carinate lobe on the posterolateral margin in contrast to the absence of teeth or lobes on the posterolateral margin; (3) paired mesobranchial lobes situated well inside the posterolateral margin unlike those of *Pseudohepatis-cus* which are submarginal; and (4) the anterolateral margin separated from the orbit by a sulcus unlike the anterolateral margin of *Pseudohepatiscus* which is continuous with the orbit.

MATUTITES ANTHONYAE, n. sp.
Plate 3, Figure 3

Diagnosis: As for genus.

Etymology: This species is named for Irene C. Anthony, former reference librarian of the Natural History Branch, Smithsonian Institution Libraries, in appreciation for her years of extraordinary library assistance to the authors.

Holotype: (USNM 484554), cl 17.5 mm, cw 15.1 mm.

Type locality: USGS 26883, M.M. Berkeley Quarry, Berkeley County, South Carolina. Santee Limestone.

Occurrence: Santee Limestone, South Carolina.

PSEUDOHEPATISCUS, n. gen.

Diagnosis: Carapace broadly obovate, length slightly less than width, broadest at fourth anterolateral denticle; dorsal surface uneven, regions defined by 8 large protuberances, posterior 2 submarginal. Front appearing weakly projecting, width slightly less than 1/4 carapace width. Fronto-orbital width subequal to half carapace width. Orbit subcircular, marginal, produced at exorbital margin. Anterolateral margin continuous with orbit, entire, not divided into teeth or lobes by incisions, distinctly scalloped along edge in lateral view, margin with single row of denticles; row interrupted by 5 equally spaced, larger denticles, latter at high points of scalloped edge in lateral view. Posterolateral margins straight, strongly convergent posteriorly, lacking teeth or lobes. Posterior margin truncate, very narrow, width less than width of front.

Type species: Pseudohepatiscus marinoi, n. sp., by present designation and monotypy.

Etymology: Pseudo, from the Greek, *pseudos,* fallacy or lie, in combination with the generic name *Hepatiscus.* Gender masculine.

Remarks: Pseudohepatiscus can be differentiated from *Hepatiscus* s.s. at once by: (1) its carapace outline which shows a steeper more convergent, anterolateral margin and a straight, not concave as in *Hepatiscus* s.s., posterolateral margin; (2) its scalloped anterolateral margin (as seen in lateral view); (3) the presence of eight, dorsal protuberances, not six as in *Hepatiscus;* and (4) the absence of a suborbital flank like that found in *Hepatiscus,*

Eriosachila, Osachila, Hepatus, and *Hepatella.*

The relationship of *Pseudohepatiscus* to *Matutites* was discussed above. *Pseudohepatiscus* differs from *Eriosachila* in lacking the suborbital flank distinctive of the latter genus and its allies.

PSEUDOHEPATISCUS MARINOI, n. sp.
Plate 3, Figure 4

Diagnosis: As for genus.

Etymology: This species is named for Cesare R. Marino, anthropologist, NMNH, in appreciation for his translation of scientific Italian, which contributed significantly to this paper.

Holotype: (USNM 484555), cl 11.5 mm, cw 12.5 mm.

Type locality: USGS 26879, M.M. Georgetown Quarry, Georgetown County, South Carolina. Santee Limestone.

Occurrence: Santee Limestone, South Carolina.

Family MAJIDAE Samouelle, 1819

WILSONIMAIA, n. gen.

Diagnosis: Size moderately large (cl more than 36.4 mm). Carapace very elongate, bottle- or flask-shaped, strongly arched transversely, flattened adjacent to posterior margin, length, measured from base of rostral notch, about 2 times width. Regions well-defined, separated by deep grooves. Fronto-orbital margin slightly more than half carapace width. Orbits only slightly produced laterally, moderately small. Dorsal surface very uneven, with numerous unequal tubercles. Urogastric and cardiac regions unusually long, combined length about half length of carapace. Posterior gastric pits situated just anterior to cervical groove, well anterior to midline or about 2/3 distance from posterior margin.

Type species: Wilsonimaia ethelae, n. sp., by present designation.

Etymology: This genus is named for Druid Wilson, stratigrapher and paleontologist, formerly of the P & S Branch, USGS, and the NMNH, in recognition of his numerous contributions to Atlantic and Gulf Coastal Plain stratigraphy and paleontology. In addition, Druid Wilson discovered the type specimen of the type species.

Included species: Wilsonimaia ethelae, n. sp. and *W. schneiderorum,* n. sp.

Remarks: Among fossil crabs, *Wilsonimaia* superficially resembles only one genus, *Micromaia* Bittner, 1875, from which it can be immediately distinguished on the basis of its carapace proportions alone. The ratio of cl to cw of *W. ethelae* is about 0.49; if its rostrum were complete this ratio might be as low as 0.44. In contrast, the cl to cw ratios for species of *Micromaia* range from a high of 0.86 to a low of 0.66. Beschin *et al.* (1985) figure all of the then known species of *Micromaia* and give cl to cw ratios for each.

Wilsonimaia is distinct from all known living majid genera.

WILSONIMAIA ETHELAE, n. sp.
Plate 3, Figure 5

Diagnosis: Very similar to *Wilsonimaia schneiderorum* in carapace outline but with fewer, shorter, less prominent, and more widely spaced tubercles.

Etymology: This species is named for the late Ethel Wilson, wife and field companion of many years to Druid Wilson, in recognition of her significant contribution to the collections of the NMNH through her husband, and in appreciation for her encouragement and support of the senior author's research.

Holotype: (USNM 484561), cl 36.4 mm, cw 18.5 mm.

Type locality: USGS 22329, Irrigation pit, about 0.2 km W of Northeast Cape Fear River, Pender County, North Carolina. Castle Hayne Limestone.

Occurrence: Castle Hayne Limestone, North Carolina.

Remarks: Wilsonimaia ethelae differs from *W. schneiderorum* in having: (1) about 1/3 fewer dorsal tubercles; (2) longer, more prominent tubercles; and (3) more inflated mesogastric, urogastric, and cardiac regions

WILSONIMAIA SCHNEIDERORUM, n. sp.
Plate 3, Figure 6

Diagnosis: Very similar to *Wilsonimaia ethelae* in carapace outline but with more numerous, closely spaced dorsal tubercles.

Etymology: This species is named for Judith Raynor Schneider and her husband, Vincent Schneider, of Garner, North Carolina for their contribution to North Carolina paleontology.

Judith Schneider collected the holotype of this new taxon.

Holotype: (USNM 484562), cl 37.3 mm, cw 24.2 mm.

Type locality: USGS 26872, Ideal Cement Company Quarry, New Hanover County, North Carolina. Castle Hayne Limestone.

Occurrence: Castle Hayne Limestone, North Carolina.

Remarks: Wilsonimaia schneiderorum is easily separated from *W. ethelae* by: (1) a distinctly greater number of dorsal tubercles, about 1/3 more than *W. ethelae;* (2) low, blunt tubercles in contrast to the longer, more prominent tubercles found on *W. ethelae;* and (3) its less inflated mesogastric, urogastric and cardiac regions.

Family CANCRIDAE Latreille, 1803

SANTEECARCINUS, n. gen.

Diagnosis: Palm short, thin, highest distally. Superior surface produced into greatly incurved, crest-like margin with 2 strong marginal spines. Outer surface of palm granulate. Ventral margin incurved. Inner surface of palm very convex; superior margin with broad, moderately deep sulcus; inferior margin with very deep, narrow sulcus. Carpus short, subquadrate with very strong spine at inner superior angle.

Type species: Santeecarcinus harmatuki, n. sp., by present designation and monotypy.

Etymology: The name is formed by combining the first word of the stratigraphic unit, Santee Limestone, with the generic name *Carcinus.* Gender masculine.

Remarks: In general outline, *Santeecarcinus* compares well with a number of the figures of both fossil and living representatives of the genus *Cancer* Linnaeus, 1758, presented by Nations (1975).

Other characters that might support its placement in or near the genus *Cancer* include: (1) the very incurved, somewhat

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PLATE 4

Figures

1. *Santeecarcinus harmatuki* Blow and Manning, n. gen. and sp.
   Holotype, carpus and incomplete propodus of right chela in outer view (fixed finger and dactylus lacking), (USNM 488558), combined length 34.1 mm, prh 18.2 mm, and prt 7.8 mm. Scale = 2 mm.
   Locality: USGS 26873, New Hanover County, North Carolina. Castle Hayne Limestone.
2. *Sarahcarcinus campbellorum* Blow and Manning, n. gen. and sp.
   Holotype, incomplete right half of carapace in dorsal view, (USNM 488559), cl 13.5 mm, cw 12.3 mm, cw (to midline) 9.4 mm. Scale = 2 mm.
   Locality: USGS 26883, Berkeley County, South Carolina. Santee Limestone.

3-4. *Acantholambrus baumi* Blow and Manning, n. gen. and sp.

   3. Holotype, left half of incomplete carapace in dorsal view, (USNM 484556), cl 21.7 mm, cw 27.5 mm. Scale = 2 mm.
   Locality: USGS 26882, Berkeley County, South Carolina. Santee Limestone.
   4. Paratype, right carapace margin with nearly complete branchial projection in dorsal view, (USNM 484557), cl 18.9 mm, cw 28.2 mm. Scale = 2 mm.
   Locality: USGS 26883, Berkeley County, South Carolina.
   Santee Limestone.

5. *Viacarcinus druidi* Blow and Manning, n. gen. and sp.
   Holotype, carapace in dorsal view (front and orbits incomplete), (USNM 484559), cl 7.3 mm, cw 10.1 mm. Scale = 2 mm.
   Locality: USGS 26883, Berkeley County, South Carolina. Santee Limestone.
6. *Laevicarcinus dockeryi* Blow and Manning, n. sp.
   Holotype, incomplete carapace in dorsal view (front and right anterolateral margin lacking), (USNM 484579), cl 12.8 mm, cw 17.9 mm. Scale = 2 mm.
   Locality: USGS 26883, Berkeley County, South Carolina. Santee Limestone.
7. *Eohalimede walleri* Blow and Manning, n. gen. and sp.
   Holotype, silicone cast of incomplete external mold of carapace in dorsal view (front lacking), (USNM 484580), cl 11.8 mm, cw 15.2 mm. Scale = 2 mm.
   Locality: USGS 26883, Berkeley County, South Carolina. Santee Limestone.

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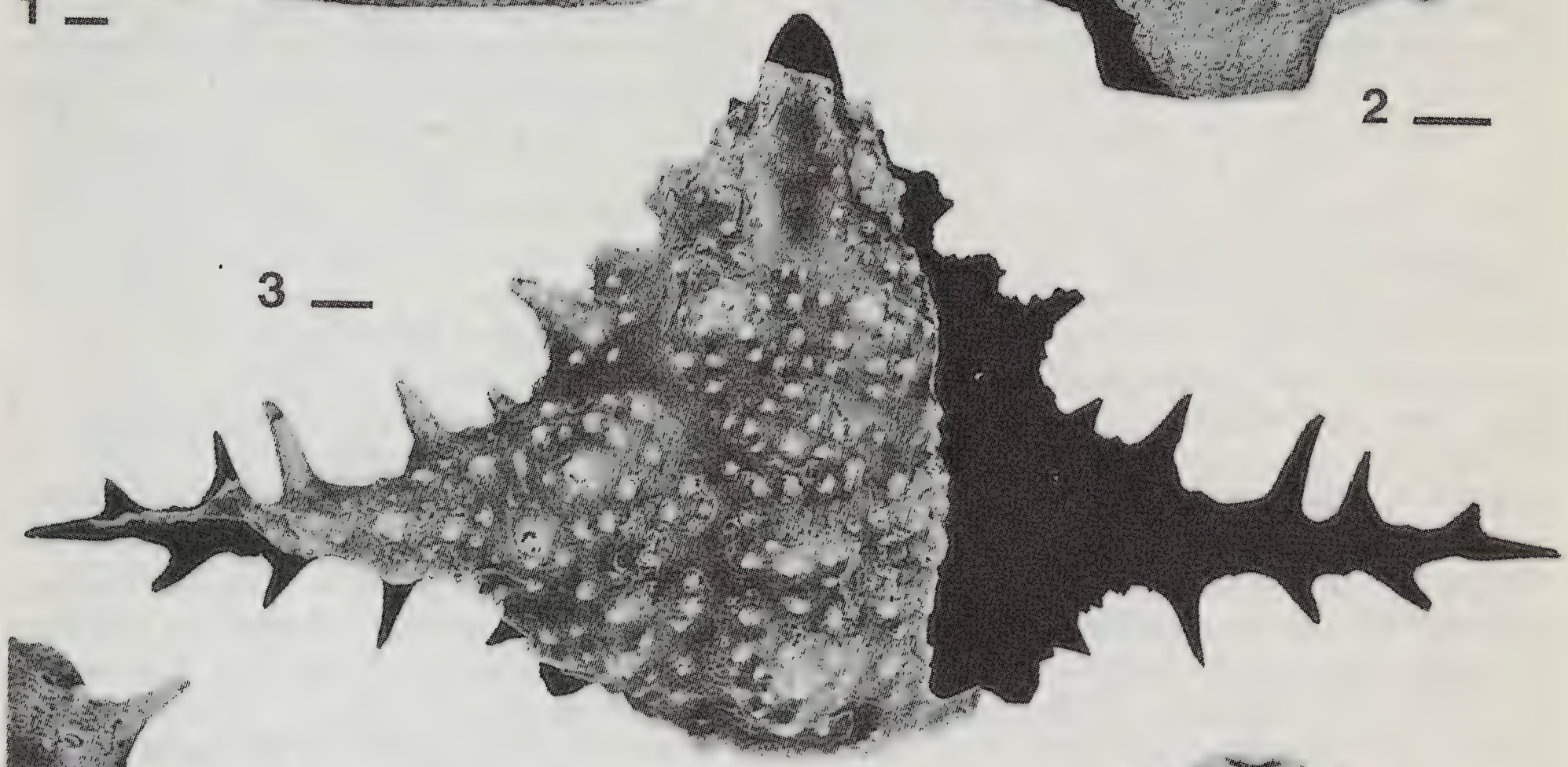
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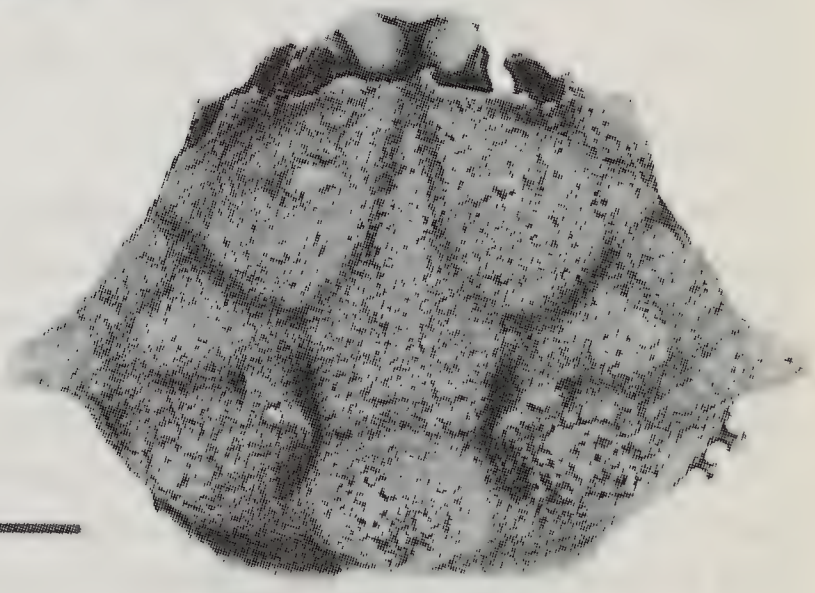
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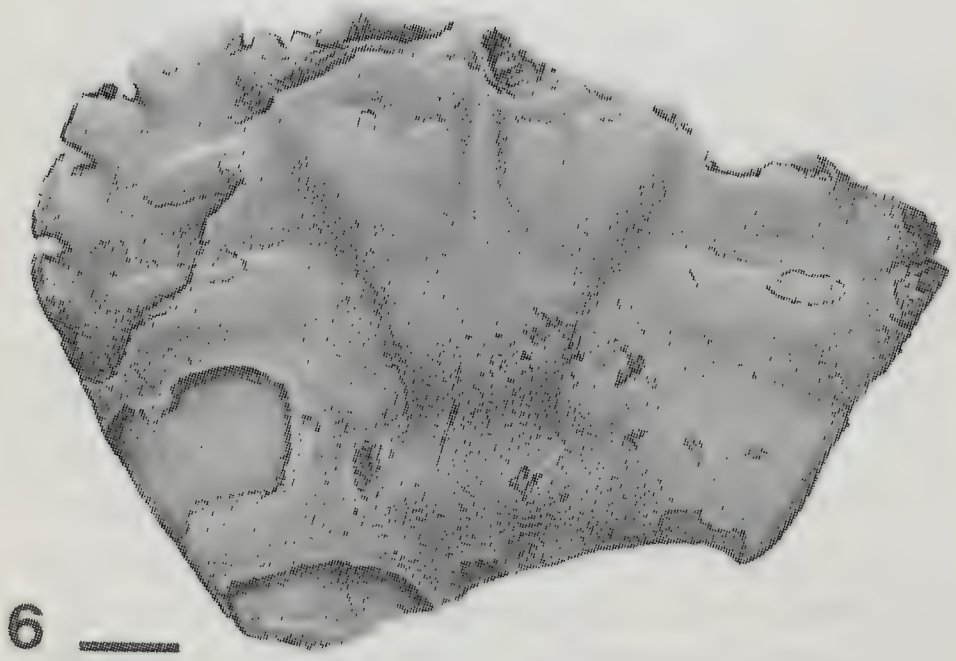
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PLATE 4

flattened superior surface of the palm, which is produced into a crest-like margin; (2) its very prominent carpal spine; (3) the uneven or roughened appearance of its carpus, and (4) the granulated outer surfaces of both its carpus and palm. However, the two strong spines on the margin of the ridge of its superior surface and the very deep sulcus along its inner, inferior margin are both very atypical of the genus *Cancer.* It is principally on the bases of these latter two points that we erect this new genus.

SANTEECARCINUS HARMATUKI, n. sp.
Plate 4, Figure 1

Diagnosis: As for genus.

Etymology: This species is named for the collector of the holotype, Peter J. Harmatuk, in appreciation of his tireless efforts to enrich the collections of the NMNH.

Holotype: Right carpus and propodus (USNM 488558), combined length of carpus and propodus 34.1 mm, prh 18.2 mm, prt 7.8 mm.

Type locality: USGS 26873, Ideal Cement Company Quarry, New Hanover County, North Carolina. Castle Hayne Limestone.

Occurrence: Castle Hayne Limestone, North Carolina.

SARAHCARCINUS, n. gen.

Diagnosis: Carapace broadly subhexagonal, broadest at fifth anterolateral tooth; outer orbital tooth and 7 upturned, acute, anterolateral teeth paired on 4 broad lobes separated by deep fissures. Fronto-orbital margin broad, about 2/3 carapace width; orbit very broad. Regions well-defined, strongly elevated along and adjacent midline; urogastric and cardiac regions separated from branchial region by deep grooves; cardiac region medially sulcate, forming 2 distinct ridges. Dorsal surface coarsely granulate nearly everywhere, distinctly depressed behind anterolateral teeth.

Type species: Sarahcarcinus campbellorum, n. sp., by present designation and monotypy.

Etymology: This genus is named for Sarah Cottrill Campbell, in recognition of her contribution to Atlantic Coastal Plain paleontology.

Remarks: The inherent characters of *Sarahcarcinus* strongly suggest affinities with the family Portunidae, but it lacks the transverse ridge leading to a strong lateral tooth found on so many portunids. In addition its rough, coarsely granulate, uneven dorsal surface, highly elevated regions along and adjacent to its midline, including a very high cardiac region with a median sulcus (separating 2 ridges), and paired anterolateral teeth are atypical of members of the Portunidae. Combinations of these characters are more typical of some species included in the diverse genus *Cancer* Linnaeus, 1758. Based on these similarities with *Cancer,* we place *Sarahcarcinus* in the family Cancridae with some reservation, given the absence of a complete front, orbit and associated chela for this new genus. *Sarahcarcinus campbellorum* like a number of species included in the genus *Cancer,* differs dramatically from the type of the genus, *C. pagurus* Linnaeus, 1758, and on this basis we erect this new genus.

SARAHCARCINUS CAMPBELLORUM, n. sp.
Plate 4, Figure 2

Diagnosis: As for genus.

Etymology: This species is named for the family of Lyle D. Campbell, his wife Sarah and their three sons David, Matthew, and Andrew, all paleontologists, of Spartansburg, South Carolina, in recognition of their combined contribution to Atlantic Coastal Plain paleontology.

Holotype: (USNM 488559), cl 13.5 mm, cw 12.3 mm, cw (to midline) 9.4 mm.

Type locality: USGS 26883, M. M. Berkeley Quarry, Berkeley County, South Carolina. Santee Limestone.

Paratype: (USNM 488560), cl 12.3 mm, cw 18.0 mm; locality USGS 26883, as above. Santee Limestone.

Occurrence: Santee Limestone, South Carolina.

Family PARTHENOPIDAE MacLeay, 1838

ACANTHOLAMBRUS, n. gen.

Diagnosis: Carapace broadly ovate-pentagonal, with extremely long, thorny, laterally-directed branchial projections. Length of carapace, equal to half greatest width (including projections). Regions well-defined, inflated; medial spine of hepatic, protogastric, cardiac, and metabranchial regions very prominent; surface uneven, very spinous. Front subtriangular, broad at base, strongly projecting anteriorly. Orbital hiatus broad, deep, apparently extending to base of suborbital lobe; basal antennal

article missing, no evidence of its fusion to suborbital lobe or front visible. Orbits small, subcircular, composed of 4 lobes; sub-marginal supraorbital eave separated from laterally produced, post-orbital lobe by distinct intercalated spine. Carapace constricted behind orbits.

Type species: Acantholambrus baumi, n. sp., by present designation and monotypy.

Etymology: The name is formed by combining the Latin *acanthus,* thorny, with the generic name *Lambrus.* Gender masculine.

Remarks: The carapace outline, including the very long branchial projections, and the strong intercalated spine of the orbit of *Acantholambrus* immediately distinguish it from all other extinct and Recent genera of the family Parthenopidae.

Acantholambrus has the longest branchial projections of any parthenopid known to us. In outline its shape is rivaled only by that of the European Eocene majid *Periacanthus* Bittner, 1875.

ACANTHOLAMBRUS BAUMI, n. sp.
Plate 4, Figures 3-4

Diagnosis: As for genus.

Etymology: This species is named for Gerald R. Baum, stratigrapher, University of South Carolina, Columbia, in recognition of his contribution to the stratigraphy of the middle Eocene of North and South Carolina. In addition, Gerald Baum helped collect the holotype of this new taxon.

Holotype: (USNM 484556), cl 21.7 mm, cw 27.5 mm.

Type locality: USGS 26882, M.M. Berkeley Quarry, Berkeley County, South Carolina. Santee Limestone.

Paratypes: (USNM 484557), cl 18.9 mm, cw 28.2 mm; (USNM 484558) cl 15.9 mm, cw 17.4 mm; (484557-484558), locality USGS 26883, same quarry as above. Santee Limestone.

Occurrence: Santee Limestone, South Carolina.

Family EUMEDONIDAE Neumann, 1878

VIACARCINUS, n. gen.

Diagnosis: Carapace broadly pentagonal with prominent, short spine at each anterolateral angle where carapace broadest; regions well-defined, surfaces covered with mushroom-like tubercles. Subhepatic regions swollen, extending well beyond carapace outline; subhepatic and protogastric regions each with remnants of a single blunt protuberance; protogastric regions unusually large; mesogastric region broad, distinctly pentagonal basally, length about 2/3 length of carapace; anterior extension unusually broad. Cardiac region greatly inflated, hemispherical. Orbit weakly projecting, composed of 4 lobes; suborbital lobe very prominent.

Type species: Viacarcinus druidi, n. sp., by present designation and monotypy.

Etymology: A combination of the surname Via with the generic name *Carcinus.* This genus is named for the late Father Luis Via Boada. Gender masculine.

Remarks: Among the Recent Eumedonidae, *Viacarcinus* most closely resembles the genus *Eumedonus* H. Milne Edwards, 1834, and, in particular, *E. granulosus* MacGilchrist, 1905. *Viacarcinus* can be, however, immediately separated from *Eumedonus* on the bases of its: (1) distinctive pentagonally shaped and proportionally longer and broader mesogastric region; and (2) greatly inflated subhepatic regions. In addition, the more complex and more projecting orbital margin of *Viacarcinus* is composed of four lobes in contrast to the simple, nearly uninterrupted marginal orbit of *Eumedonus.* Also, the orbits of *Viacarcinus* are situated more anteriorly than the orbits in *Eumedonus,* and unlike *Eumedonus* and nearly all members of the Eumedonidae, the anterolateral margin of *Viacarcinus* is distinctly longer than its posterolateral margin.

Viacarcinus represents the first fossil member of the family Eumedonidae to be recognized as well as the first North American member of the family.

VIACARCINUS DRUIDI, n. sp.
Plate 4, Figure 5

Diagnosis: As for genus.

Etymology: This species is named for Druid Wilson, formerly of the P & S Branch, USGS, who discovered it.

Holotype: (USNM 484559), cl 7.3 mm, cw 10.1 mm.

Type locality: USGS 26883, M.M. Berkeley Quarry, Berkeley County, South Carolina. Santee Limestone.

Paratype: (USNM 484560) cl 7.0 mm, cw 10.0 mm; locality USGS 25865, same quarry as above. *In situ,* near the top of the Santee

Limestone.

Occurrence: Santee Limestone, South Carolina.

Family XANTHIDAE Dana, 1851

EOCARPILIUS, n. gen.

Diagnosis: Carapace transversely oval, very convex, length about 3/4 carapace width, broadest just anterior to midline; regions not defined. Anterolateral margin entire, narrow, decorated with a single row of small beads. Front broad, more than 1/3 carapace width, greatly deflexed, quadrilobate. Orbit sub-circular, marginal; margin entire, not raised or thickened, outlined by single row of small beads. Antennae missing; basal antennal article apparently short, narrow anteriorly, robust at base, as inferred from length and shape of orbital hiatus. Chela unequal in males; major chela of male massive, palm short, distinctly highest distally; fixed finger with two teeth; minor chela of male much smaller and more narrow than major, highest at proximal end.

Type species: Eocarpilius carolinensis, n. sp., by present designation.

Etymology: The name is formed by combining the Greek *eos,* dawn, with the generic name *Carpilius.* Gender masculine.

Included Species: Eocarpilius carolinensis and *Eocarpilius anomala* (Rathbun, 1935), n. comb., middle Eocene, North Carolina.

Remarks: Eocarpilius is remarkably similar to the extant genus *Carpilius* Leach, *in* Desmarest, 1823, with which it appears most closely allied. It can, however, be separated immediately from *Carpilius* on the basis of its anterolateral angle alone, which lacks the strong tooth and accompanying short, transverse, dorsal ridge distinctive of *Carpilius.* In addition, *Eocarpilius* differs from *Carpilius* in having: (1) a transversely more highly arched carapace; (2) a relatively narrow anterolateral margin; (3) a weak postorbital angle lacking the strong, postorbital tooth distinctive of *Carpilius;* (4) weak orbital margins; (5) well separated, submedial frontal lobes unlike those of *Carpilius* which are produced into a single, thickened, upturned process; and (6) two teeth on the fixed finger of the right chela.

Eocarpilius can also be easily distinguished from *Palaeocarpilius* s.s., which it resembles superficially. Unlike *Palaeocarpilius,* the carapace of *Eocarpilius* has: (1) no dorsal transverse ridge at the anterolateral angle; (2) no anterolateral teeth or lobes; (3) a distinctly quadrilobate front, with the submedial lobes well separated and only slightly extending below the lateral lobes; and (4) a relatively short

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PLATE 5

Figures

1-2. *Eocarpilius carolinensis* Blow and Manning, n. gen. and sp.
1. Male holotype, articulated specimen in ventral view, (USNM 484563), cl 53.4 mm, cw 69.2 mm; right propodus prl 50.1 mm, prh 28.5 mm, prt 15.7 mm; left propodus prl 34.3 mm, prh 14.5 mm, prt (covered). Scale = 4 mm.
Locality: USGS 26883, Berkeley County, South Carolina. Santee Limestone.
2a. Paratype, carapace in dorsal view, (USNM 484565), cl 41.7 mm, cw 53.2 mm. Scale = 4 mm.
2b. Paratype, carapace in anterior view, (USNM 484565). Scale = 4 mm.
Locality: USGS 26884, same quarry as 26883 above. Santee Limestone.

3. *Santeella lillyae* Blow and Manning, n. gen. and sp.
Holotype, internal mold of carapace in dorsal view (surface with remnants of weathered cuticle), (USNM 484578), cl 4.4 mm, cw 5.2 mm. Scale = 0.5 mm.
Locality: USGS 26883, Berkeley County, South Carolina. Santee Limestone.

4. *Santeexanthus wardi* Blow and Manning, n. gen. and sp.
Holotype, incomplete carapace in dorsal view (right orbit and right anterolateral margin lacking), (USNM 484575), cl 13.3 mm, cw 18.9 mm. Scale = 2 mm.
Locality: USGS 26883, Berkeley County, South Carolina. Santee Limestone.

5. *Titanocarcinus purdyi* Blow and Manning, n. sp.
Male holotype, internal mold of carapace in dorsal view (surface with remnants of weathered cuticle), (USNM 484571), cl 19.5 mm, cw 21.5 mm. Scale = 2 mm.
Locality: USGS 26883, Berkeley County, South Carolina. Santee Limestone.

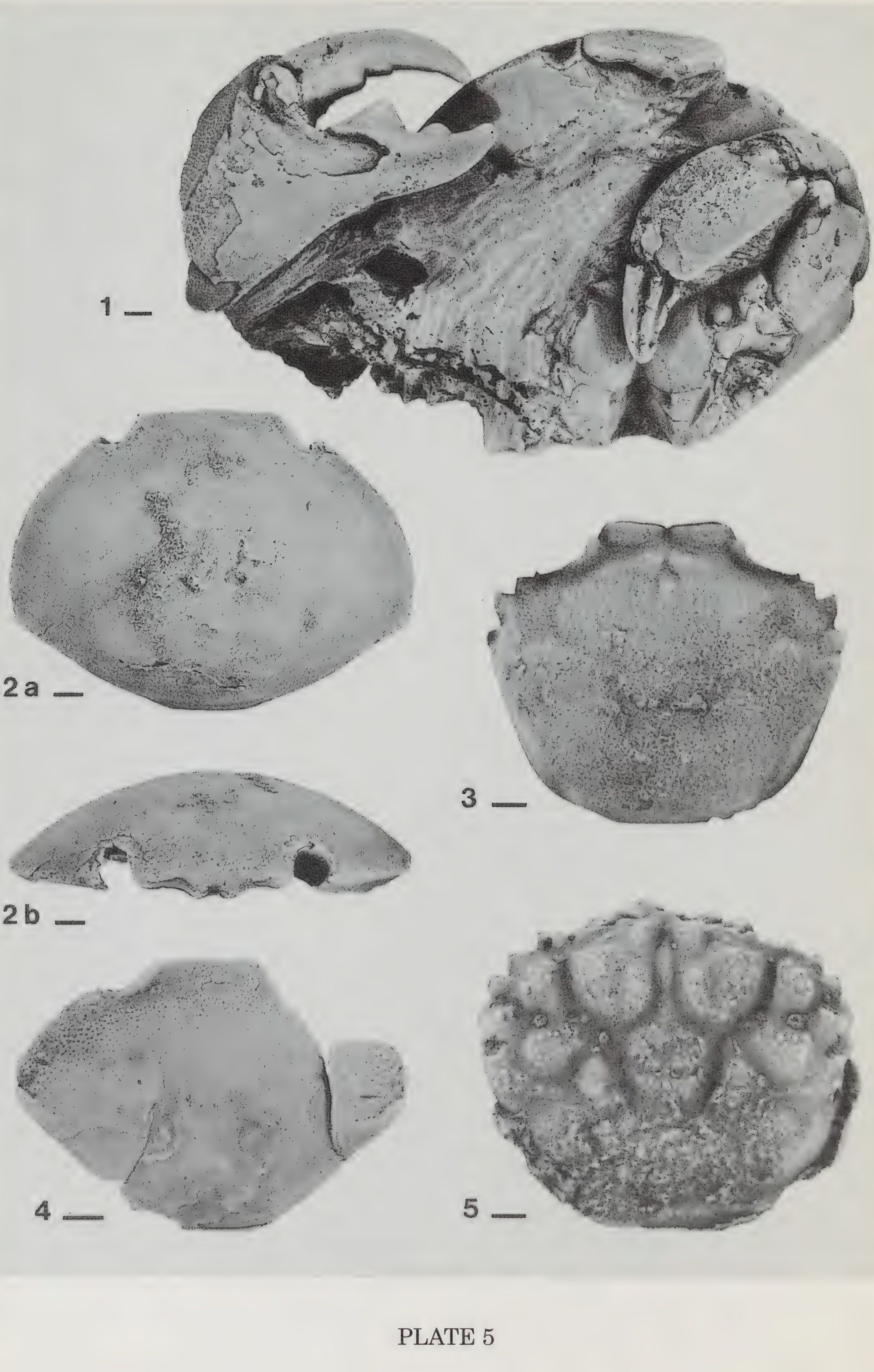

PLATE 5

orbital hiatus and an apparent, broad antennal base.

EOCARPILIUS CAROLINENSIS, n. sp.
Plate 5, Figures 1-2

Diagnosis: As for genus. Exception, see remarks below.

Etymology: The specific name *carolinensis* refers to the states of North and South Carolina in which this species is commonly found.

Holotype: (USNM 484563), cl 53.4 mm, cw 69.2 mm; right propodus prl 50.1 mm, prh 28.5 mm, prt 15.7 mm; left propodus prl 34.3 mm, prh 14.5 mm, prt (covered).

Type locality: USGS 26883, M.M. Berkeley Quarry, Berkeley County, South Carolina. Santee Limestone.

Paratypes: (USNM 484565), cl 41.7 mm, cw 53.2 mm; locality USGS 26884, same quarry as USGS 26883, above. Santee Limestone.

(USNM 484566), cl 38.9 mm, cw 49.3 mm; (USNM 484567) cl 42.3 mm, cw 58.5 mm; (USNM 484568), cl 29.4 mm, cw 41.5 mm, estimated cw 42.6 mm; (USNM 484569), cl 25.1 mm, cw 24.8 mm; estimated cw 32.1 mm; right propodus (USNM 484570), prl 32.5 mm, prh 23.7 mm, prt 12.5 mm; right propodus (USNM 488561) prl 32.5 mm, prh 23.1 mm, prt 12.3 mm; (USNM 484566-484570 and 488561), locality USGS 26878, M.M. Georgetown Quarry, Georgetown County, South Carolina. Santee Limestone.

(USNM 484564), cl (estimate) 60.0 mm, cw (estimate) 82.0 mm; right propodus prl 65.4 mm, prh 36.3 mm, prt 18.5 mm; locality USGS 26875, Atlantic Limestone Co., Maple Hill, Pender County, North Carolina [locality data suspect]. Castle Hayne Limestone.

In addition, two paratypes have been deposited in the VMNH.

Occurrence: Castle Hayne Limestone, North Carolina; Santee Limestone, South Carolina.

Remarks: The palm of the major or right chela of our new species, *E. carolinensis,* agrees in general form with the incomplete right palm of the holotype and only specimen of *E. anomala* (Rathbun) (see Rathbun, 1935, p. 87, as *Menippe anomala*). It is so similar to Rathbun's species that we initially regarded it as conspecific with her species. *Eocarpilius carolinensis,* however, differs from *E. anomala* in having: (1) much smaller, more numerous and more closely spaced tubercles along its superior margin; (2) a slightly steeper slope to its superior margin; and (3) the inner surface of the palm of *E. carolinensis* is less inflated than that of *E. anomala.*

EOHALIMEDE, n. gen.

Diagnosis: Carapace suboctagonal, width greater than length, broadest at anterolateral angle; regions well-defined, surfaces finely granulate; dorsolateral, medial, and posterior surfaces ornamented with large, mushroom-shaped prominences, appearing cauliflower-like dorsally. Fronto-orbital width much more than half carapace width. Frontal width about 1/3 carapace width. Protogastric region broadly subcircular, not subdivided into lobes. Anterolateral margin with 3 mushroom-shaped prominences.

Type species: Eohalimede walleri, n. sp., by present designation and monotypy.

Etymology: The name is formed by adding the Greek *eos,* dawn, to the generic name *Halimede.* Gender feminine.

Remarks: Eohalimede is remarkably similar to the Recent genus *Halimede* de Haan, 1835. It appears to be the closest fossil relative of *Halimede. Eohalimede* differs from *Halimede* s.s. in having: (1) a broader fronto-orbital width which is much greater than half the carapace width; (2) a broader frontal width which is about one-third the carapace width; (3) broadly subcircular protogastric regions which are neither subdivided nor covered with large prominences; and (4) three anterolateral, equally spaced, dorsally rounded, mushroom-shaped prominences.

EOHALIMEDE WALLERI, n. sp.
Plate 4, Figure 7

Diagnosis: As for genus.

Etymology: This species is named for Thomas R. Waller, paleomalacologist, NMNH, in recognition of his contribution to paleobiology and with particular appreciation for his encouragement, advice, and for sharing his laboratory space with the authors.

Holotype: (USNM 484580), cl 11.8 mm, cw 15.2 mm.

Type locality: USGS 26883, M.M. Berkeley Quarry, Berkeley County, South Carolina. Santee Limestone.

Paratypes: (USNM 484581), cl 12.1 mm, cw 11.9 mm; locality USGS 26882, same quarry as

USGS 26883, above. Santee Limestone.

Occurrence: Santee Limestone, South Carolina.

LAEVICARCINUS DOCKERYI, n. sp.
Plate 4, Figure 6

Diagnosis: Carapace subhexagonal, flattened, width much greater than length, regions distinct. Fronto-orbital width about half carapace width. Anterolateral margin divided into 4 broad teeth separated by deep incisions; second tooth only about half width of first. Posterolateral margins with distinct notch placed well behind fourth anterolateral tooth. Dorsal surface punctate, lateral teeth and lateral margins coarsely granulate. Cervical groove well marked, forming broad V on carapace. Hepatic and epibranchial regions each with a single, long, coarsely granulated, oblique transverse ridge. Protogastric region with 2 short, unaligned, granulated ridges.

Etymology: This species is named for David T. Dockery, Mississippi Geological Survey, in recognition of his contribution to the paleontology and stratigraphy of the Paleogene deposits of the southeastern United States, with an emphasis on Mississippi.

Holotype: (USNM 484579), cl 12.8 mm, cw 17.9 mm.

Type locality: USGS 26883, M.M. Berkeley Quarry, Berkeley County, South Carolina. Santee Limestone.

Occurrence: Santee Limestone, South Carolina.

Remarks: Laevicarcinus dockeryi closely resembles the type and only other remaining, recorded species of *Laevicarcinus, L. egerensis* Lörenthey, in Lörenthey and Beurlen, 1929, from the late Eocene of Hungary, a species from which it can be easily separated. *Laevicarcinus dockeryi,* unlike *L. egerensis,* has: (1) a second anterolateral tooth only about half the width of the first; (2) two, short, unaligned ridges on each protogastric region; and (3) coarsely granulated anterolateral and posterolateral margins.

This is the first record outside of Hungary for a member of this genus as well as the first American record for the genus.

SANTEELLA, n. gen.

Diagnosis: Size very small (cl 4.4 mm). Carapace subhexagonal, flattened transversely, length more than 4/5 width, broadest at third anterolateral tooth; regions not strongly defined. Front strongly produced anteriorly, transverse, bilobed, width less than half carapace width. Orbit wide, sloping posteriorly; outer orbital tooth minute. Anterolateral margin divided into 4 distinct teeth, all anterior to midlength. Posterolateral margins steep, not strongly convergent posteriorly.

Type species: Santeella lillyae, n. sp., by present designation and monotypy.

Etymology: The name is formed by combining the first word of the stratigraphic unit, Santee Limestone, with the diminutive suffix *-ella.* Gender feminine.

Remarks: Given its small size and the limited information provided by its internal mold, *Santeella lillyae* cannot be placed in any living or fossil genus or family with certainty at this time. It resembles some members of both the families Goneplacidae and Xanthidae. We place this new genus in the family Xanthidae with some reservation and base this family placement principally on the similarities of its orbit and anterolateral margin to those characteristic of members of this family.

SANTEELLA LILLYAE, n. sp.
Plate 5, Figure 3

Diagnosis: As for genus.

Etymology: This species is named for Lilly King Manning, in recognition of her vast contribution to systematic crustacean research through her thousands of scientific illustrations and in appreciation for her ongoing support.

Holotype: (USNM 484578), cl 4.4 mm, cw 5.2 mm.

Type locality: USGS 26883, M.M. Berkeley Quarry, Berkeley County, South Carolina. Santee Limestone.

Occurrence: Santee Limestone, South Carolina.

SANTEEXANTHUS, n. gen.

Diagnosis: Carapace transversely oval; length about 2/3 carapace width; regions indistinct; dorsal surface without grooves or furrows, densely punctate anteriorly. Fronto-orbital

margin about 2/3 carapace width. Anterolateral margin nearly straight, cristate, divided into 3 lobes and single distinct dentiform tooth.

Type species: Santeexanthus wardi, n. sp., by present designation and monotypy.

Etymology: The name is formed by combining the first word of the stratigraphic unit, Santee Limestone, with the generic name *Xantho.* Gender masculine.

Remarks: The overall appearance of *Santeexanthus* clearly suggests that it is a member of the family Xanthidae, but it compares poorly with all known fossil genera of this family. It more closely resembles some Recent xanthids, such as *Paratergatis longimanus* Sakai, 1965, but on close inspection these similarities are only superficial.

SANTEEXANTHUS WARDI, n. sp.
Plate 5, Figure 4

Diagnosis: As for genus.

Etymology: This species is named for Lauck W. Ward, stratigrapher and paleontologist, Virginia Museum of Natural History, Martinsville, Virginia, in recognition of his significant and ongoing contribution to the paleontology and stratigraphy of the Atlantic Coastal Plain with an emphasis on Virginia and North Carolina. In addition, Lauck Ward provided some of the specimens cited in this paper.

Holotype: (USNM 484575), cl 13.3 mm, cw 18.9 mm.

Type locality: USGS 26883, M.M. Berkeley Quarry, Berkeley County, South Carolina. Santee Limestone.

Paratypes: (USNM 484576), cl 10.9 mm, cw 15.2 mm; (USNM 484577) cl 17.0 mm, cw 24.6 mm; all locality USGS 26883, as above. Santee Limestone. In addition a paratype has been deposited in the VMNH.

Occurrence: Santee Limestone, South Carolina.

TITANOCARCINUS PURDYI, n. sp.
Plate 5, Figure 5

Diagnosis: Carapace subquadrate, width slightly greater than length, broadest at third lateral tooth, regions well-defined, moderately swollen; cervical groove distinct. Fronto-orbital width much more than half carapace width. Frontal lobes separated by very deep sinus, latter flanked by strongly projecting frontal spines followed laterally to orbit by smaller spines. Lower orbital margin with 5 acute spines. Anterolateral margin slightly longer than posterolateral margin; lateral margin with 5 primary teeth. Outer orbital tooth through third lateral tooth armed anteriorly with thin, branching, apically blunt, projections; fourth and fifth lateral teeth incomplete. Dorsal surface punctate, superior surfaces of regions often appear granulate and/or armed with short, blunt spines. Protogastric region longitudinally sulcate to base, length about 1/4 carapace length. Mesogastric region low, flattened, greatest width about 1/4 carapace width; anterior extension narrow, long.

Etymology: This species is named for Robert W. Purdy, paleontologist, NMNH, in recognition of his contribution to Atlantic Coastal Plain paleontology and in particular for his contribution of specimens to this study.

Holotype: (USNM 484571), cl 19.5 mm, cw 21.5 mm.

Type locality: USGS 26883, M.M. Berkeley Quarry, Berkeley County, South Carolina. Santee Limestone.

Paratypes: (USNM 484572), cl 23.5 mm, cw 25.8 mm; (USNM 484573), cl 15.9 mm, cw 17.2 mm; (USNM 484574), cl 15.9 mm, cw 13.4 mm: all locality USGS 26883, as above. Santee Limestone.

Occurrence: Santee Limestone, South Carolina.

Remarks: Titanocarcinus purdyi can be distinguished from the only other American species, *T. natchitochensis* (Stenzel, 1935) (originally described in *Lobonotus* A. Milne Edwards, 1863), from the middle Eocene of Louisiana, in having a much smaller, more rounded epibranchial region and the upper surfaces of its regions appear granulate or finely spinous while those of *T. natchitochensis* are covered with large, closely spaced pustules.

The carapace of *T. aculeatus* Busulini *et al.,* 1984, figured by those authors (1984, pls. 1-3), unlike a number of its congeners, is fully intact and represented by the original cuticle. The long fronto-orbital and lateral spines seen in these figures of *T. aculeatus* are very similar to those found in the limestone surrounding the internal mold of the holotype of *T. purdyi. Titanocarcinus purdyi* can, however, be easily separated from *T. aculeatus* by its more quadrate carapace and much nar-

rower mesogastric and cardiac regions. In addition, the fronto-orbital and lateral spines of *T. purdyi* are not as long or acute as those of *T. aculeatus,* and, unlike *T. aculeatus,* they are sometimes bifurcate on the lateral margin.

V. LOCALITY DATA

The following are USGS Cenozoic locality numbers. Locality numbers, where combined, indicate only that their respective collections were made at the same geographic locality; collectors, collecting dates, and stratigraphic horizons and/or locations within a quarry may vary between locality numbers. All specimens were collected as "spoil" unless otherwise indicated.

NORTH CAROLINA: CASTLE HAYNE LIMESTONE

USGS 26870. M.M. Castle Hayne (formerly Superior Stone Company) quarry, N side secondary road 1002, 2.2 miles (3.5 km) E 25° N of US 117 and secondary road 1002 intersection in Castle Hayne, New Hanover Co., N.C.

USGS 26871. Locality as USGS 26870 above. W end of pit.

USGS 26872, 26873. Ideal Cement Company quarry, N side of secondary road 1002, (quarry center) 4.2 miles (6.7 km) E 20° N of US 117 and secondary road 1002 intersection in Castle Hayne, New Hanover Co., N.C.

USGS 22329. Spoil bank of irrigation pit about 0.1 mile (0.2 km) S on W side of first dirt road turning off N.C. Rte. 210 (Lane Ferry Road) at a point about 0.1 mile (0.2 km) W of Northeast Cape Fear River, Pender Co., N.C.

USGS 26874. Maple Hill (Lanier Pit), 2.6 miles (4.1 km) S 23° E of NC Rte. 50 and secondary road 1520 intersection in Maple Hill, and 0.75 mile (1.2 km) S 20° W of NC Rte. 50 and secondary road 1532 intersection, Pender Co., N.C.

USGS 26875. Maple Hill (Atlantic Limestone Quarry), Pender Co., N.C. (locality data suspect).

USGS 26876. Billy B. Fussel Company, Inc., quarry, 1.5 miles (2.4 km) S of US 117 and secondary road 1102 intersection in Rose Hill, and 0.5 mile (0.8 km) W of US 117 on S side of secondary road 1148, Duplin Co., N.C.

SOUTH CAROLINA: SANTEE LIMESTONE

USGS 26878, 26879, 26880, 26881. M.M. Georgetown (= Jamestown) quarry, approx. 2.8 mile (4.5 km) N 33° E of Jamestown, on W side U.S. 17A, Georgetown Co., S.C.

USGS 26882, 26883, 26884. M.M. Berkeley (= Cross) quarry, approx. 5.3 miles (8.5 km) SE of Eutawville, and about 2.2 miles (3.5 km) S 20° E of S.C. Rtes. 6 and 45 intersection with secondary hwy 59 (Berkeley-Orangeburg Co. line road) on E side of secondary hwy 59, Berkeley Co., S.C.

USGS 25865. Locality as 26882 above. *In situ:* Top 9 inches of soft Santee Limestone, about 4 feet below overlying Cross Formation.

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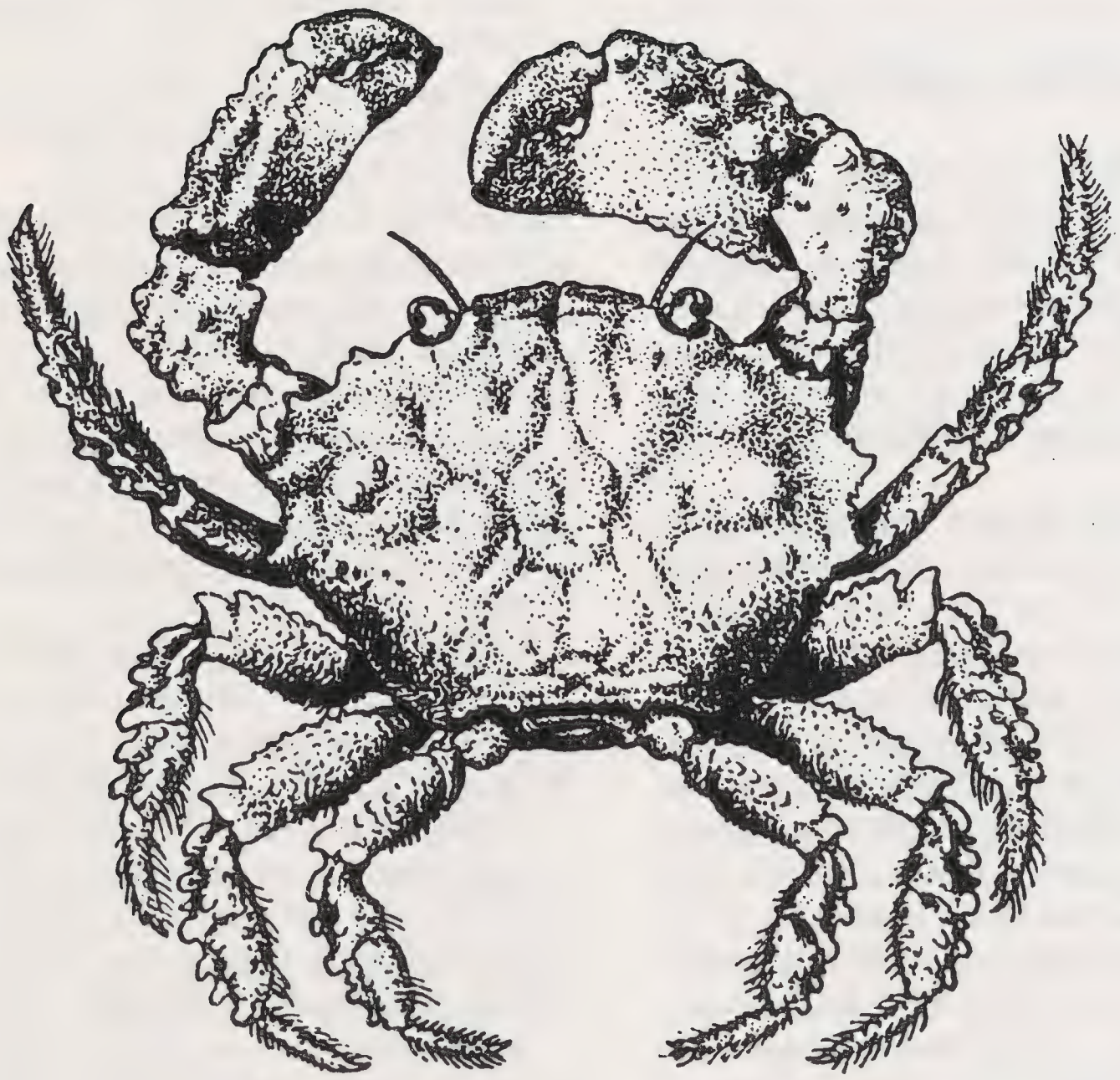

TULANE STUDIES IN GEOLOGY AND PALEONTOLOGY

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CENOZOIC MURICIDAE OF THE WESTERN ATLANTIC REGION PART XI – THE SUBFAMILY ERGALATAXINAE

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I. ABSTRACT

The muricid subfamily Ergalataxinae has only recently been recognized to comprise a small number of primarily Indo-Pacific genera and species, which have been placed in a variety of subfamilies over the years. In the western Atlantic the group is poorly represented with but six species in all. One, assigned to the genus *Cytharomorula*, is a relatively deep-water form known only from the Recent fauna. Three species are assigned to the genus *Trachypollia*. Of these, one occurs in the Oak Grove Sand, the Shoal River Formation, and (?) the Gatun Formation; one is from the Cercado, (?)Caloosahatchee, Bowden, Moín, and Bermont formations and the Recent fauna; and one is found only in the Recent fauna. Two species are assigned to the genus *Lindapterys,* one from the Miocene Chipola Formation and one from the Pleistocene Moín Formation and the Recent fauna.

II. INTRODUCTION

In studying the gastropod family Muricidae, once one leaves the well-defined subfamilial groups of Muricinae, Muricopsinae, and Typhinae, suprageneric assignments become not a little complicated. There is still no clear consensus as to which genera should be assigned to the Ocenebrinae, the Trophoninae, or the Rapaninae (= Thaidinae of authors). In addition to these long accepted groups, we must add another more recently proposed subfamily, which is the least well-defined of the entire family Muricidae. Although most subfamilial taxa have been recognized since the turn of the Century (primarily Cossmann, 1903), this subfamily was only delineated in 1971 by Kuroda, Habe, and Oyama.

The members of the subfamily Ergalataxinae are, for the most part, non-varicate muricids, and are probably the most misunderstood species in the entire family. As a measure of just how misunderstood this collection of species actually is, they were originally named in at least 48 different genera, including the types of nine new genera. The genera in which the various species were described include not only *Murex, Ocenebra, Urosalpinx,* and *Trophon*, but also *Drupa* (including the synonyms *Ricinula, Pentadactylus,* and *Sistrum*), *Purpura, Triton [= Cymatium], Buccinum, Cantharus, Nassarina, Fusus, Peristerina,* and *Latirus* to mention but a few.

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The group is primarily Indo-Pacific in distribution but there are New World species and this paper is an attempt to bring together the few representatives of the subfamily in the western Atlantic. Two of the genera in the Western Hemisphere have a respectable fossil record, stretching back to the Early Miocene but, on the whole, the group is poorly represented in both the fossil and Recent faunas of the western Atlantic.

Characters that unite members of this subfamily include a radula that is muricine in appearance but with a strongly recurved rachidian plate much like that of the Muricopsinae. The operculum is half-way between that of the typical Muricinae, with a basal nucleus, and the purpuroid type, with a lateral nucleus, found in the Ocenebrinae and Rapaninae (= Thaidinae). This operculum with a sub-basal nucleus is the same type found in the Trophoninae, which is why many of the species were originally described as "*Trophon*."

In general, members of this group tend to have a large, open aperture, usually denticulate on the outer lip and frequently on the inner lip. In most, the siphonal canal is short, often the spire is half the shell length. And, most importantly, as noted above, the shells are non-varicate or, if they do have varices, these tend to be irregular in appearance, often just the apertural lip is thickened in the adult stage.

III. ACKNOWLEDGMENTS

My heartfelt gratitude is expressed to the staff of several institutions for the material utilized in this study. The Natural History Museum [formerly the British Museum (Natural History)], Recent Mollusca Section (Kathie Way, especially), kindly permitted me to search their collections seeking members of this misunderstood group, and to photograph those that were located, as did the Institut Royal des Sciences Naturelles de Belgique. The United States National Museum of Natural History (M.G. Harasewych, Raye N. Germon, Thomas R. Waller, Warren C. Blow) kindly lent specimens for study, as did the Academy of Natural Sciences of Philadelphia (Gary Rosenberg, David G. Robinson), Houston Museum of Natural Science (John Wise, Constance Boone), and the Florida Museum of Natural History (Roger W. Portell). Edward J. Petuch, Florida Atlantic University, Bernard Landau, Albufeira, Portugal, and the Coltro brothers, Jose and Marcus, of Sao Paulo, Brazil, provided other specimens for illustration. To Roland Houart, Landen, Belgium, I owe more than mere words can say, as we have worked on the taxonomic problems of the Ergalataxinae together over the years. And, finally, my most sincere thanks to Andrew and Greta Murray, Bradenton, Florida, who not only provided valuable material of *Trachypollia trachea* but also recognized the species as one named by Gardner, sparing me the embarrassment of creating yet another synonym in this already over-described group. Zuzana Hruska, of the Tulane University Coordinated Instrumentation Facility, provided the SEM photographs.

ABBREVIATIONS FOR REPOSITORY INSTITUTIONS

BMNH – Museum of Natural History [British Museum (Natural History)], London, England
HMNS – Houston Museum of Natural Science, Houston, TX
IRSNB – Institut Royal des Sciences Naturelles de Belgique, Bruxelles, Belgium
MCZ – Museum of Comparative Zoology, Harvard University, Cambridge, MA
NMB – Naturhistorisches Museum, Basel, Switzerland
TU – Tulane University, New Orleans, LA
UF – Florida Museum of Natural History, Gainesville, FL
USNM - United States National Museum of Natural History, Washington, DC

IV. SYSTEMATIC PALEONTOLOGY

Family MURICIDAE Rafinesque, 1815
Subfamily ERGALATAXINAE Kuroda, Habe, and Oyama, 1971

Genus CYTHAROMORULA Kuroda, 1953

Cytharomorula KURODA, 1953, Venus, v. 17, p. 183.

Type species: *Cytharomorula vexillum* Kuroda, 1953, by monotypy.

CYTHAROMORULA GRAYI (Dall)
Plate 1, figures 1-7

Nassaria (Nassarina) grayi DALL, 1889, Harvard Mus. Comp. Zool., Bull., v. 18, p. 183, pl. 32, fig. 12a.

Cantharus (Tritonidea) laevis E.A. SMITH, 1890, Zool. Soc. London, Proc., 1890, pt. 2, p. 261, pl. 21, fig. 11.

Trophon lowei WATSON, 1897, Jour. Linn. Soc., v. 26, p. 244, pl. 19, fig. 12.

"Nassarina" grayi Dall. WOODRING, 1928, Carnegie Inst. Washington, Publ. 385, p. 269.

Evokesia grayi (Dall). RADWIN and D'ATTILIO, 1972, Biol. Soc. Washington, Proc., v. 85, no. 28, p. 336; RADWIN and D'ATTILIO, 1976, Murex Shells of the World, p. 143, pl. 23, fig. 4 (USNM 94778a); KAICHER, 1979, Card Cat. World-Wide Shells, pack no. 20 (Muricidae–Part 4), no. 1977.

Urosalpinx lowei (Watson). NORDSIECK, 1975, La Conchiglie, An. 7, nos. 75-76, p. 5, fig. 22.

Nassarina grayi Dall. NORDSIECK, 1975, La Conchiglie, An. 7, nos. 75-76, p. 5, fig. 25.

Orania grayi (Dall). BOUCHET and WARÉN, 1985, Boll. Malac., Suppl. 1, p. 150, figs. 344 (radula), 356.

Cytharomorula grayi (Dall). HOUART, 1991, Nautilus, v. 105, no. 1, p. 33; HOUART and ABREU, 1994, Apex, v. 9, no. 4, p. 122, figs. 5 (holotype–*Trophon lowei* Watson), 6; HOUART, 1995, Bull. Mus. Natl. Nat. Hist., Paris, (Ser. 4) v. 16 (1994), Sect. A, nos. 2-4, p. 254, figs. 9, 10 (radula), 67, 68.

Cytharomorula sp. cf. *C. grayi* (Dall). TRONDLE and HOUART, 1992, Apex, v. 7, nos. 3-4, p. 89, fig. 48.

Cytharomorula gravi [*sic*] (Dall). RIOS, 1994, Seashells of Brazil, ed. 2, p. 114, pl. 37, fig. 480.

Citharomorula [*sic*] *grayi* (Dall). COLTRO, 1995, La Conchiglia, An. 27, no. 275, p. 49, color fig. 3.

Description: "Shell solid, strong, yellowish white with darker brown spiral lines and about six whorls. Nucleus smooth brown; sculpture of numerous close-set spiral threads, of which about every third or fourth is stronger and darker colored than the others; transverse sculpture of stout ribs becoming obsolete behind the periphery, thus giving the whorl a shouldered aspect, there are nine or ten of these on the last whorl, extending well forward; the rib behind the aperture is varicoid and swollen; the spiral sculpture passes over the ribs, which are a little angulate at the periphery; the whorl is appressed to the suture, which in the upper whorls is more or less waved by the ends of the ribs behind it; the aperture is long, narrow, and somewhat contracted, the continuous margin less elevated than in the preceding species [*Nassarina columbellata* Dall]; the base of the last whorl is somewhat constricted, the canal is twisted, recurved, and with a strong siphonal fasciole; the outer lip has about seven teeth of which the hinder ones are the stronger; there is a rounded callus on the body and also a few denticulations on the anterior part of the columella." (Dall, 1889, p. 183)

Lectotype: MCZ 7256; height 12.0 mm, diameter 5.8 mm (*fide* Dall, 1889, p. 183; not found, 1993) (here designated).

Type locality: Blake Station 290, off Barbados in73 fathoms [133.5 meters] (here designated).

Occurrence: Recent only, Canary Islands, Madeira, St. Helena, and Lesser Antilles to southern Brazil. Also Indian Ocean, French Polynesia, and New Caledonia (Trondle and Houart, 1992, p. 88; Houart, 1995, p. 254).

Figured specimens: Fig. 1, USNM 869667; height 17.0 mm, diameter 8.8 mm; locality, Las Palmas, Canary Islands, dredged in 120-200 meters. Fig. 2, USNM 94778a (paralectotype); height 15.3 mm, diameter 7.6 mm; locality, *Blake* Station 290, off Barbados. Fig. 3, USNM 94778b (paralectotype); height 11.8 mm, diameter 6.0 mm; locality, *Blake* Station 290, off Barbados. Fig. 4, BMNH 89.10.1 [holotype–*Cantharus (Tritonidea) laevis* E.A. Smith]; height 22.3 mm, diameter 10.0 mm; locality, St. Helena. Fig. 5, Dautzenberg Collection (IRSNB); height 20.4 mm, diameter 10.1 mm; locality, St. Helena. Fig. 6, BMNH 1911.7.17.2 [holotype–*Trophon lowei* Watson]; height 19.2 mm, diameter 9.8 mm; locality, Madeira, 50 fathoms [91 meters]. Fig. 7, BMNH; height 18.8 mm, diameter 10.3 mm; locality, Porto Santo, Madeira, 60 fathoms [110 meters].

Discussion: It is interesting that this moderately deep-water species should have received three names in the short period from 1889 to 1897. It also is characteristic of the entire subfamily that the three species should have been named in three different genera, as this has been the fate of most of the species now referred to the Ergalataxinae. Like most of the

species in the subfamily, *C. grayi* is extremely variable; in general, becoming more elongate with increasing size (*e.g.*, pl. 1, fig. 4). There are usually reddish-brown spiral lines topping the spiral cords, and often a broad reddish band anterior to the shoulder. Some specimens develop small nodules at the intersection of the axial and spiral ornamentation (*e.g.*, pl. 1, fig. 1).

The type lot consists of six specimens taken by the *Blake*, of which two are at the U.S. National Museum of Natural History (USNM 94778, both from Station 290; figured here pl. 1, figs. 2, 3), and four are at the Harvard Museum of Comparative Zoology. Dall's figured specimen is MCZ 7256; however, the specimen in the box with that label is not *C. grayi* but another species (as noted by Trondle and Houart, 1992, p. 89). This is not the only muricid type specimen that is missing in the MCZ collections, as has been previously discussed (see Vokes, 1992, p. 50). It is apparent that at some time between 1945, when Clench and Pérez Farfante studied the Muricidae of the western Atlantic, and about 1970, when Radwin and D'Attilio (1976, p. 31) attempted to study the holotype of *Murex carnicolor,* someone engaged in nefarious activity, removing the type specimens of at least two species (*Murex carnicolor* Clench and Pérez Farfante and *Nassarina grayi* Dall). These specimens have not been simply mislaid, for in each case a specimen of a different species with the *same approximate dimensions* has been substituted in the box. This suggests deliberate larceny. Certainly a dedicated search through the entire muricid collection in 1993 did not locate these missing types.

This poses a dilemma, for Dall did not designate a type specimen for *Nassarina grayi*. He cited the measurements of the figured example, but then added "a larger but imperfect specimen is 15.5 mm long" (Dall, 1889, p. 183). This is the specimen here figured in pl. 1, fig. 2, which is from *Blake* Station 290, as is also indicated on the label for the supposed "type" at MCZ. Nevertheless, in the perhaps misguided hope that the figured specimen will someday be found, I am designating that specimen as the lectotype. The original illustration (Dall, 1889, pl. 32, fig. 12b) is excellent and there is no question as to the identity of the species. In the MCZ collections there are also three other examples (MCZ 7258, from Station 152; MCZ 7259, from Station 272; and MCZ 7257, no station number). Of the six specimens in the type lot, five are from off Barbados, in 73, 76, and 100 fathoms [= 133, 139, 183 meters] and MCZ 7258 is from St. Kitts, in 127 fathoms [232 meters].

Trophon lowei and *Cantharus laevis* were described from Madeira and St. Helena, respectively, and the species is

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PLATE 1

Figures Page

1-7. *Cythraromorula grayi* (Dall). 29

1. (X 3) USNM 869667; height 17.0 mm, diameter 8.8 mm.
   Locality: Las Palmas, Canary Islands, dredged in 120-200 meters; Recent.
2. (X 3) USNM 94778a (paralectotype); height 15.3 mm, diameter 7.6 mm.
   Locality: *Blake* Station 290, off Barbados; Recent.
3. (X 4) USNM 94778b (paralectotype); height 11.8 mm, diameter 6.0 mm.
   Locality: *Blake* Station 290, off Barbados; Recent.
4. (X 2.5) BMNH 89.10.1 [holotype – *Cantharus (Tritonidea) laevis* E.A. Smith]; height 22.3 mm, diameter 10.0 mm.
   Locality: St. Helena; Recent.
5. (X 2.5) Dautzenberg Collection (IRSNB); height 20.4 mm, diameter 10.1 mm.
   Locality: St. Helena; Recent.
6. (X 3) BMNH 1911.7.17.2 [holotype – *Trophon lowei* Watson]; height 19.2 mm, diameter 9.8 mm.
   Locality: Madeira, 50 fathoms [91 meters]; Recent.
7. (X 3) BMNH; height 18.8 mm, diameter 10.3 mm.
   Locality: Porto Santo, Madeira, 60 fathoms [110 meters]; Recent.

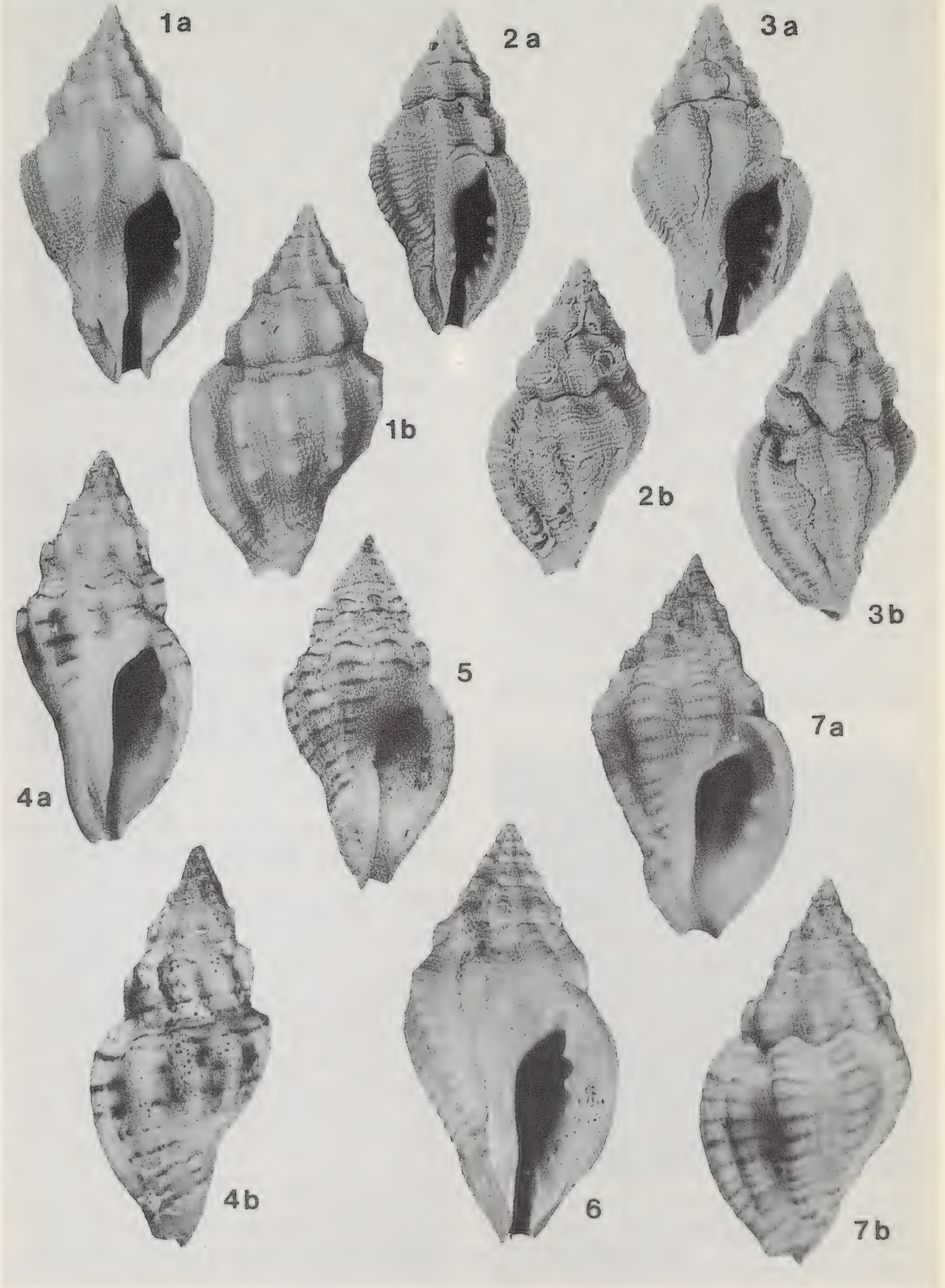


PLATE 1

commonly taken by shrimp trawlers off the Canary Islands (pl. 1, fig. 1) in depths of 120-200 meters. In the collection of the Museu Oceanográfico Rio Grande do Sul there are numerous examples from off the coast of Brazil, as far south as the state of Rio Grande do Sul (Rios, 1994, pl. 37, fig. 480; Coltro, 1995, color fig. 3). Thus, the range of the species seems to encompass the entire tropical and sub-tropical zone of the Atlantic Ocean, both eastern and western, in depths on the order of 100-200 meters. In addition, Trondle and Houart (1992, p. 88, fig. 48) and Houart (1995, p. 254, figs. 67, 68) have demonstrated that the identical form is also living in the Indian Ocean and the southwestern Pacific Ocean. It appears that this is a world-wide tropical species.

Genus TRACHYPOLLIA Woodring, 1928

Trachypollia WOODRING, 1928, Carnegie Inst. Washington, Publ. 385, p. 268.

Type species: *Trachypollia sclera* Woodring, 1928, by original designation (and monotypy).

Morunella EMERSON and HERTLEIN, 1964, San Diego Soc. Nat. Hist., Trans., v. 13, no. 17, p. 361.

Type species: *Buccinum lugubre* C.B. Adams, 1852, by original designation.

Discussion: Radwin and D'Attilio (1972, p. 328) were the first to recognize the muricid affiliation of the genus *Trachypollia*, which Woodring had considered to be "close to *Pollia*' Sowerby," a buccinid. In addition to *T. sclera* they included *Buccinum lugubre* C.B. Adams, 1852, *Drupa didyma* Schwengel, 1943, and *Purpura nodulosa* C.B. Adams, 1845. All four species have a papillose multiwhorl protoconch (see text-figures 1-5) and a radula that is similar to both the ergalataxine genus *Orania* and the rapanine genus *Morula*.

Initially, I followed these authors in assigning "*Purpura*" *nodulosa* Adams to *Trachypollia* (Vokes, 1983, p. 50, fig. 5; Vokes and Vokes, 1983, p. 23, pl. 13, fig. 1; Vokes, 1984, p. 214, pl. 2, figs. 26, 27) but shell characters in this species do not match those of *Trachypollia*. Additional work indicates that this common and widespread species (one of the few occurring in both the eastern and western Atlantic) is better referred to the rapanine genus *Morula*.

Another group that has been confused with *Trachypollia* is the muricopsine subgenus *Muricopsis (Risomurex),* which also has a non-varicate, beaded shell, and denticles on both the inner and outer apertural lips. However, the latter may be distinguished not only by the radula but by the protoconch, which is always of one and one-half, usually (but not always) keeled whorls, and by having the fourth labral denticle (counting from anterior to posterior) somewhat larger than the others.

TRACHYPOLLIA TRACHEA (Gardner)
Plate 3, figures 1-3
Text-figure 1

Nassarina trachea GARDNER, 1944, U.S. Geol. Survey, Prof. Paper 142-G, p. 465, pl. 50, fig. 21.

[?] *Trachypollia aneureta* WOODRING, 1964, U.S. Geol. Survey, Prof. Paper 306-C, p. 258, pl. 42, figs. 8, 9.

Description: "Shell small but rather heavy, fusiform. Aperture approximately half the total height. Whorls closely coiled, increasing regularly in diameter, feebly convex; the body smoothly but rather abruptly constricted at the base, conch including only 4 3/4 turns in the type but containing 5 in a less perfect adult. Protoconch rather small and slender, smooth, polished, conic in outline, the initial turn worn away but apparently minute and almost entirely submerged, the 3 extant nuclear whorls broadly rounded, all of them moderately elevated, and increasing rather rapidly in diameter. Dividing line between conch and protoconch sharply indicated by a change in the texture of the shell and by the abrupt assumption of the postnuclear sculpture, both axial and spiral. Axials broadly inflated, usually 8 on the earlier whorls, 7 on the later, persisting from suture to suture and, on the body, well down to the base, regular in size and spacing except on the last half turn in some adults. Interaxial areas sharply concave and narrower than the axials. Spiral sculpture overriding the axial; primary spirals rather narrow but prominently elevated, flattened upon their summits, 3 on both the earlier and the later whorls of the spire, the posterior spiral decidedly less prominent than the 2

in front of it, the anterior a little more prominent than the medial, thus lending to the whorl a somewhat trapezoidal outline. Primaries on the body and pillar 7 or 8, the 2 or 3 that gird the medial portion the most prominent; a single sharp, narrow, finely beaded secondary usually introduced between each pair of primaries, except on the medial portion of the body, where the secondary may be simple or where exceedingly fine tertiaries may be developed on either side of the primary. Incremental sculpture sufficiently strong to roughen the flattened interspiral channels and, on the base of the body and the pillar, roughening even the primaries themselves. Whorls closely appressed; the sutures distinct, undulated by the costae of the preceding whorl, in most individuals following a fourth primary on the later whorls and in some falling in front of it. Aperture lobate, obtusely angulated at the posterior commissure. Outer lip symmetrically arched between the commissure and the canal, finely crenate at the margin in harmony with the external sculpture, the inner surface reinforced with 4 or 5 elongated denticles, the medial the most prominent. Curvature at the base of the body rather strong. Parietal wall and pillar smoothly glazed, the pillar denticulate in the adult. Columella simple. Anterior canal not very long, the margins parallel and slightly recurved. Anterior fasciole sharply differentiated, incrementally striated, obscurely lirate, strongly arched, and obliquely emarginate at its extremity." (Gardner, 1944, p. 465)

Holotype: USNM 371810; height 8.3 mm, diameter 4.1 mm.

Type locality: USGS 4742, Shoal River Formation; Shell Bluff, Walton County, Florida (= TU 69)

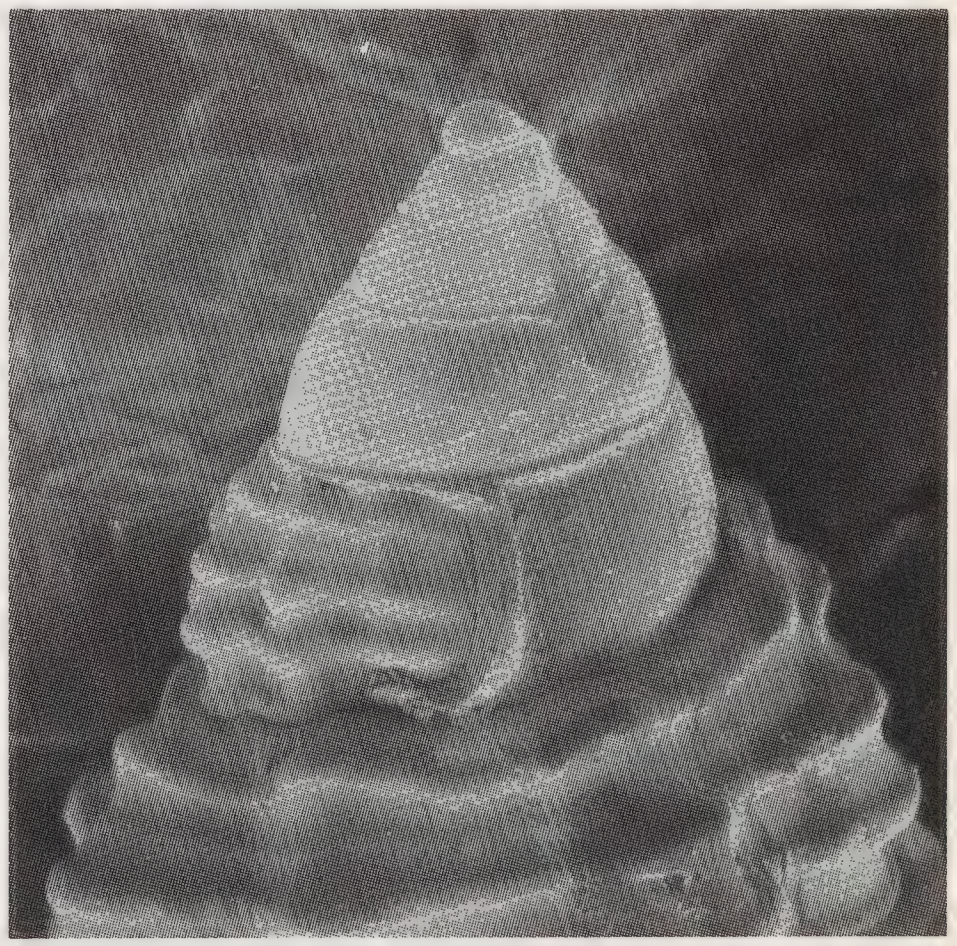
Occurrence: Oak Grove Sand, Shoal River Formation, Florida; (?)Gatun Formation, Panama.

Figured specimens: Fig. 1, UF 68774; height 9.0 mm, diameter 4.1 mm; locality UF-WL004, Shoal River (NW 1/4 Sec. 4, T3N, R21W), about 3 1/2 miles north of Mossyhead, Walton Co., Florida (? = TU 69A). Fig. 2, UF 66106; height 8.8 mm, diameter 4.5 mm; locality UF-WL004. Fig. 3, UF 68775; height 8.3 mm, diameter 3.8 mm; locality TU 91. Other occurrence: TU 69A.

Discussion: In the Tulane collections we have long had four small specimens from the late Early Miocene Oak Grove Sand (TU 91), and two from the Middle Miocene Shoal River Formation (TU 69A). It was not until another, larger example from the Shoal River was collected by Roger Portell and Kevin Schindler (1993) that these were recognized as the oldest known species of *Trachypollia*. I assumed that it was an undescribed taxon until Andrew and Greta Murray suggested that it might be that named as *Nassarina trachea* Gardner. Comparison with Gardner's material showed that her holotype has an incomplete aperture, lacking the characteristic anal notch, as well as the labial denticles. But there is no doubt that our specimens are the same as her species.

We have never taken any examples in the Chipola Formation; clearly the species lived in very shallow, sandy environments. This is reflected in the fact that in our material none has the protoconch preserved. Gardner's holotype has the remnants of a *Trachypollia* protoconch with about three conical whorls, and one specimen collected by Andrew and Greta Murray has a well-preserved protoconch, which is the papillose, multiwhorl type characteristic of *Trachypollia* (text-fig. 1).

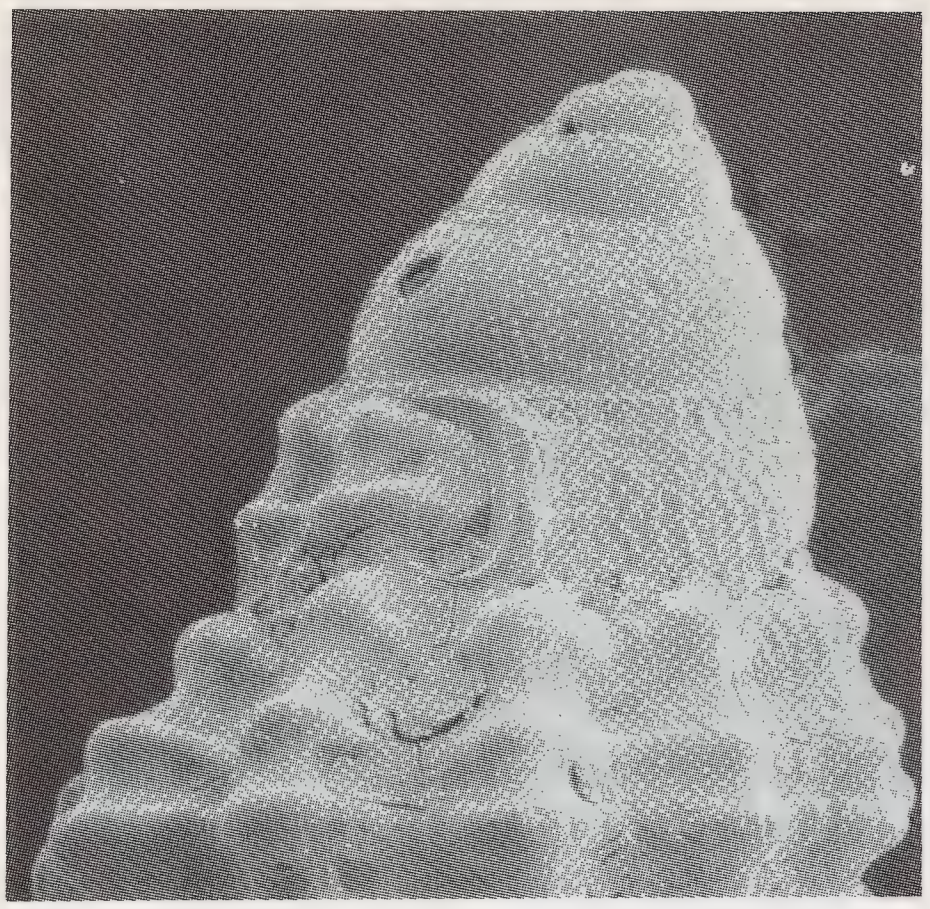
The immediately obvious difference between these Miocene specimens and the younger species of *Trachypolla* is the lack of the elaborate surface ornamentation.



Text-figure 1. *Trachypollia trachea* (Gardner); UF 68899; locality UF-WL004 (? = TU 69A) (X 40).

These shells have simple spiral cords that are not beaded except on the secondary spiral threads. However, this may be ecologically determined, as specimens from the Oak Grove Sand are more scabrous than those from Shoal River. There is a fair degree of difference in the amount of elongation of the shell between specimens of this species. As may be seen in the three examples figured here, figures 1 and 3 represent slender specimens, with a height:width ratio of 2.2:1, but figure 2 has a ratio of 2.0:1. This same variation is present in other members of *Trachypollia* (see below) and perhaps there is some sexual dimorphism in this genus, we do not know.

From the Gatun Formation of Panama, Woodring (1964, p. 258, pl. 42, figs. 8, 9) has named another small specimen (height 7.2 mm) of *Trachypollia* as *T. aneureta*. On the basis of the single incomplete holotype specimen (USNM 643651) there is no way to differentiate this species from *T. trachea*. The type of *T. aneureta* has only six axial ribs, in contrast to seven in specimens of *T. trachea,* but this does not seem to be of specific importance.



Text-figure 2. *Trachypollia sclera* Woodring; UF 68900; locality TU 1240, Moín Formation (X 40).

TRACHYPOLLIA SCLERA Woodring
Plate 2, figures 1-3
Text-figures 2, 3

Trachypollia sclera WOODRING, 1928, Carnegie Inst. Washington, Publ. 385, p. 269, pl. 16, figs. 7, 8; RADWIN and D'ATTILIO, 1972, Biol. Soc. Washington, Proc., v. 85, no. 28, p. 328, fig. 1-B; RADWIN and D'ATTILIO, 1976, Murex Shells of the World, p. 134; VOKES, 1983, Texas Conchologist, v. 19, no. 3, p. 50, fig. 1; VOKES, 1984, Shells and Sea Life, v. 16, no. 11, p. 214, pl. 2, fig. 24; PETUCH, 1994, Atlas Florida Fossil Shells, p. 132, pl. 45, fig. L [not in text].

[?] *Trachypollia didyma* (Schwengel). DE JONG and COOMANS, 1988, Stud. Fauna Curaçao, Caribbean Islands, v. 69, no. 214, p. 75, pl. 16, fig. 409 (protoconch) [? not of Schwengel].

Description: "Shell small, moderately slender, pillar short. Nucleus stout, consisting of about three smooth whorls rapidly enlarging in diameter. Aperture rather wide, contracted to form a short, wide, oblique, recurved, moderately emarginate canal. Siphonal fasciole broad, moderately inflated. Between it and edge of inner lip lies a narrow umbilical groove. Edge of inner lip standing out from pillar on adult shells. Inner lip bearing near base of columella two or three crude low denticles and also a short low parietal ridge. Interior of outer lip bearing five elongate denticles, the posteriormost one and the parietal ridge forming a posterior channel. Sculpture consisting of swollen axial ribs and of crude beaded spiral threads." (Woodring, 1928, p. 268 – description of *Trachypollia,* new genus)

"Shape, nucleus, and aperture as described above. Sculpture consisting of broad axial ribs overridden by spiral threads. Primary spirals crude, greatly swollen on summits of ribs. In each interspace on later whorls lies a fine secondary spiral." (Woodring, 1928, p. 269)

Holotype: USNM 135520; height 8.2 mm, diameter 3.8 mm.

Type locality: Bowden Formation, Bowden, Jamaica (= TU 705).

Occurrence: Cercado Formation, Dominican Republic; Bowden Formation, Jamaica; Moín Formation, Jamaica; (?)Caloosahatchee (*fide* Petuch, 1994, p. 132) and Bermont formations, Florida; Recent, Texas to Costa Rica and (?) northern South America.

Figured specimens: Fig. 1, USNM 869666; height 16.3 mm, diameter 8.0 mm; locality, off Freeport, Texas, 46 meters. Fig. 2, Landau Collection; height 11.2 mm, diameter 5.5 mm,

Text-figure 3. *Trachypollia sclera* Woodring; HMNS 39136; locality Northwest Gulf Survey Station 1375, 54.5 miles [87.8 km] southeast of Freeport, Texas, 27 fms. [49 meters] (X 40).

locality NMB 16982, Río Cana, Dominican Republic. Fig. 3, UF 68773; height 12.2 mm, diameter 6.0 mm; locality, Capeletti Pit, Dade County, Florida. Other occurrence: TU locality 1240.

Discussion: The holotype of this species is a small specimen from the Bowden Formation of Jamaica but Radwin and D'Attilio (1972) were able to recognize it as being in the same genus as *Buccinum lugubre* C.B. Adams, from the eastern Pacific, and *Drupa didyma* Schwengel, described from the east coast of Florida. After they figured these shells, along with drawings of the radula and protoconch, I was able to identify specimens collected at Moín, Costa Rica, as being living representatives of *T. sclera*.

In the collections of the Houston Museum of Natural Science there are numerous specimens taken off the Texas coast (see Vokes, 1983), which probably are responsible for both Abbott's (1974, p. 177) and Radwin and D'Attilio's (1976, p. 135) records of "*T. didyma*" from off the Texas coast. In addition, in my collection there is material from off the Dominican Republic and off the Dry Tortugas, Florida.

These Recent occurrences are duplicated in the fossil record with a single specimen taken in the Cercado Formation, Dominican Republic (pl. 2, fig. 2) and another collected by Edward J. Petuch in the Bermont Formation, Florida (pl. 2, fig. 3). In addition, Petuch (1994, pl. 45, fig. L) has figured a second specimen, also from the Capeletti pit, Bermont Formation. In the plate explanation for this specimen he notes that the species also occurs in the Caloosahatchee Formation, but I have not seen any specimens. In the Tulane collections from the Moín Formation, Costa Rica (TU 1240), we have several juvenile examples (text-figure 2).

When Schwengel described *Drupa didyma*, she stated that "the name, from the Greek, means a twin, in allusion to its resemblance to the West Coast *Drupa lugubris* (C.B. Adams)" (Schwengel, 1943, p. 76), but it is *T. sclera*, if anything, that is the "twin" to the Pacific species. The irregular ornamentation of *T. lugubris* (pl. 2, fig. 4) is more like that seen in *T. sclera* than the "beaded" appearance of *T. didyma* and the protoconch also is more like that of *T. sclera* (compare text-figs. 3 and 4).

TRACHYPOLLIA DIDYMA (Schwengel)
Plate 2, figures 5-8
Text-figure 5

Drupa didyma SCHWENGEL, 1943, Nautilus, v. 56, no. 3, p. 76, pl. 7, fig. 7; NOWELL-USTICKE, 1959, Check List Mar. Shells St. Croix, p. 63, pl. 3, fig. 14.

Morula (Morunella) didyma (Schwengel). EMERSON and HERTLEIN, 1964, San Diego Soc. Nat. Hist., Trans., v. 13, no. 17, p. 361.

Morula didyma (Schwengel). RIOS, 1970, Coastal Brazilian Seashells, p. 81 [in part, dimensions refer to specimen figured in Rios, 1975, which is *T. turricula* (von Maltzan)].

Trachypollia didyma (Schwengel). RADWIN and D'ATTILIO, 1972, Biol. Soc. Washington, Proc., v. 85, no. 28, p. 330, figs. 1-J (shell), 7 (protoconch), 8 (radula), 9 (operculum); RADWIN and D'ATTILIO, 1976, Murex Shells of the World, p. 134, pl. 3, fig. 8; KAICHER, 1980, Card Cat. World-wide Shells, pack no. 25 (Muricidae–Part 5), no. 2526; VOKES, 1983, Texas Conchologist, v. 19, no. 3, p. 50, fig. 2; ESPINOSA and ROLAN, [?] 1995, Soc. Espagnola Malac., Res. Malac. IX, p. 31.

[?] Not *Drupa* cf. *didyma* Schwengel. GIBSON SMITH and GIBSON SMITH, 1972, IV Caribbean Geol. Conf., Mem., p. 474 [? = *Muricopsis (Risomurex) withrowi* Vokes and Houart).

Morula (Trachypollia) didyma (Schwengel). ABBOTT, 1974, Amer. Seashells, ed. 2, p. 177 [in part, not fig. 1873, = *Muricopsis (Risomurex) withrowi* Vokes and Houart]; RIOS, 1975, Brazilian Marine Moll. Icon., p. 92 [in part, not pl. 26, fig. 380, = *T. turricula* (von Maltzan)]; RIOS, 1985, Seashells of Brazil, p. 92 [in part, not pl. 32, fig. 400, = *T. turricula*].

[?] Not *Trachypollia didyma* (Schwengel). DE JONG and COOMANS, 1988, Stud. Fauna Curaçao, Caribbean Islands, v. 69, no. 214, p. 75, pl. 16, fig. 409 (protoconch) [? = *T. sclera* Woodring].

Trachypollia turricula (von Maltzan). HOUART, 1991, Nautilus, v. 105, no. 1, p. 33 [in part, not of von Maltzan]; RIOS, 1994, Seashells of Brazil, ed. 2, p. 113 [in part, not all localities], pl. 37, fig. 475 [not of von Maltzan].

Morula turricula (von Maltzan). SUNDERLAND and SUNDERLAND, 1993, Amer. Conchologist, v. 21, no. 4, p. 15 [not of von Maltzan].

Description: "This small shell, of 8 1/2 rounded whorls, with well defined sutures, has a comparatively large nucleus of 3 1/2 whorls, the earlier ones glossy with fine granules along the suture, the last one covered by fine rounded papillae and terminated by a narrow, elevated, curved varix, of a light brown color. The fourth whorl begins abruptly with two spiral cords, which form nodules where the axial ribs cross. The fifth, sixth and seventh whorls have three nodular spirals, and the body, or eighth whorl, has seven of these noduled spirals. Over the larger sculpture run evenly spaced spiral granular threads, two and sometimes three between each noduled spiral. The color varies from apricot-buff to cinnamon-rufous, with the nodules a carob-brown. Aperture bluish-white within, about 2/5 the length of the shell, raquet-shaped, slightly flaring outer lip with five or six lirae, the upper three or four heavy and the two lower much fainter. The shallow anal notch is accentuated by the first lira and a tubercule on the

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PLATE 2

Figures Page

1-3. *Trachypollia sclera* Woodring 34
1. (X 3.5) USNM 869666; height 16.3 mm, diameter 8.0 mm.
Locality: off Freeport, Texas, 46 meters; Recent.
2. (X 4) Landau Collection; height 11.2 mm, diameter 5.5 mm.
Locality: NMB 16982, Río Cana, Dominican Republic; Cercado Formation.
3. (X 4) UF 68773; height 12.2 mm, diameter 6.0 mm.
Locality: Capeletti Pit, Dade County, Florida; Bermont Formation.
4. *Trachypollia lugubris* (C.B. Adams) 35
(X 4) USNM 869662; height 11.5 mm, diameter 5.5 mm.
Locality: Panama Bay, Panama; Recent.
5-8. *Trachypollia didyma* (Schwengel) 35
5. (X 4) ANSP 178763 (lectotype); height 9.5 mm, diameter 4.8 mm.
Locality: off Palm Beach, Florida, 200 feet [61 meters]; Recent.
6. (X 4) USNM 869663; height 12.3 mm, diameter 5.9 mm.
Locality: off Palm Beach, Florida, 30-45 meters; Recent.
7. (X 4) USNM 869664; height 13.3 mm, diameter 7.5 mm.
Locality: off Buzios Island, Sao Paulo, Brazil, on rubble at 40 meters depth; Recent.
8. (X 4) USNM 869665; height 13.5 mm, diameter 7.2 mm.
Locality: off Palm Beach, Florida, from reef in 52 meters; Recent.
9, 10. *Trachypollia turricula* (von Maltzan) 39
9. (X 4) USNM 859068; height 11.0 mm, diameter 4.6 mm.
Locality: Corimba, Luana, Angola; Recent.
10. (X 4) Berlin Museum 37205 (lectotype); height 12.5 mm, diameter 5.4 mm.
Locality: Ile de Gorée, Senegal; Recent.

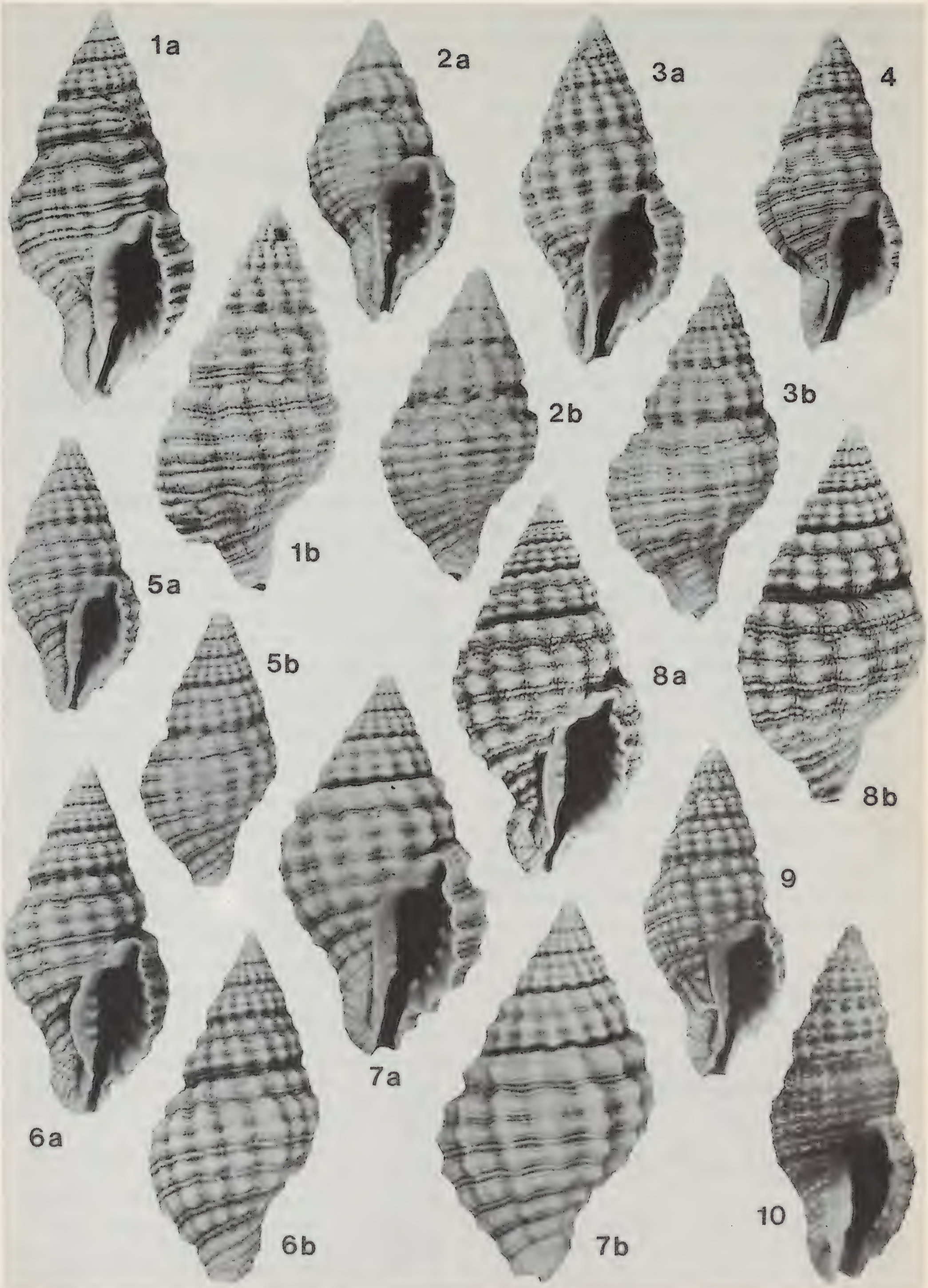


PLATE 2

heavy callus at the upper end of the parietal wall. The sigmoid columella and parietal wall are covered by a heavy reflected callus, which becomes free and erect toward the base, leaving a shallow slit or crevice in the umbilical region, and forming the outer wall of the short, deep, recurved anterior canal." (Schwengel, 1943, p. 76)

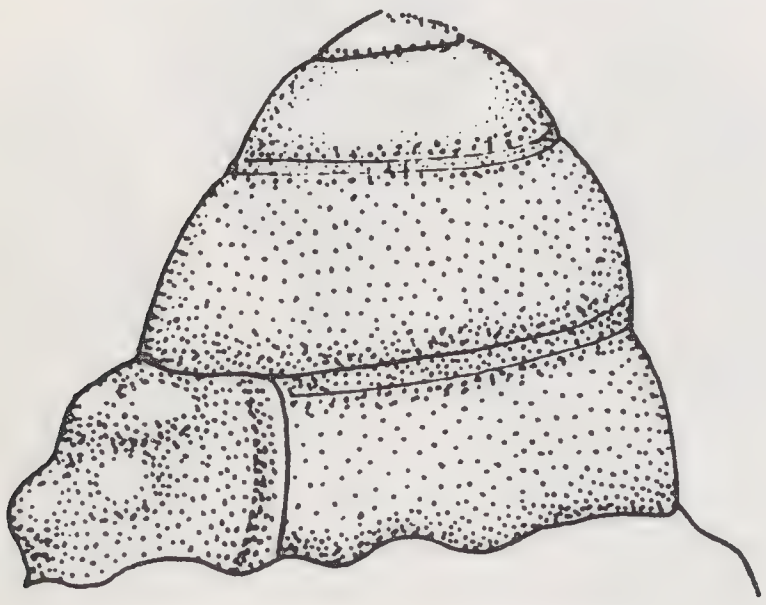
Lectotype: ANSP 178763; height 9.5 mm (protoconch broken), diameter 4.8 mm (here designated).

Type locality: off Palm Beach, Florida, dredged in 200 feet [61 meters].

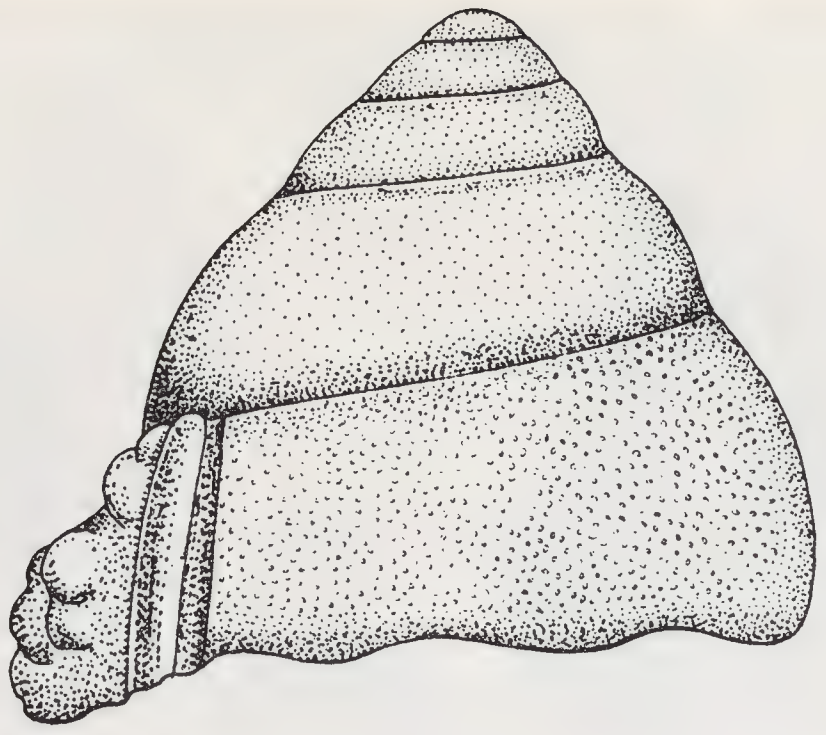
Occurrence: Recent only, Florida, Cuba, Lesser Antilles to Brazil and [?] Curaçao.

Figured specimens: Fig. 5, ANSP 178763 (lectotype). Fig. 6, USNM 869663; height 12.3 mm, diameter 5.9 mm; locality, off Palm Beach, Florida, 30-45 meters. Fig. 7, USNM 869664; height 13.3 mm, diameter 7.5 mm; locality, off Buzios Island, Sao Paulo, Brazil, on rubble at 40 meters depth. Fig. 8, USNM 869665; height 13.5 mm, diameter 7.2 mm; locality, off Palm Beach, Florida, from reef in 52 meters.

Discussion: At the Academy of Natural Sciences of Philadelphia there are three lots of this species, all from the collection of Jeanne Schwengel. The first of these is ANSP 178763, with five specimens, including the figured specimen (Schwengel, 1943, pl. 7, fig. 7), with measurements cited by Schwengel as "Length 10 mm, width 5 mm." The protoconch has been broken subsequently and the specimen now measures only 9.5 mm, but it matches the illustration exactly (except for the missing protoconch) and still retains traces of a sticky blue substance used to



Text-figure 4. *Trachypollia lugubris* (C.B. Adams); Radwin and D'Attilio, 1972, text-fig. 4.



Text-figure 5. *Trachypollia didyma* (Schwengel); Radwin and D'Attilio, 1972, text-fig. 7.

hold the shell in place for illustration. This specimen is here designated as the lectotype (pl. 2, fig. 5).

In addition to this lot there are two others labeled "paratypes," which probably were originally retained in the Schwengel Collection and only later acquired by the Academy, but all were collected by Tom McGinty in 200 feet off Palm Beach, and are presumed also to have been part of the original type lot. These are ANSP 220237, with two specimens, and ANSP 235139, with two specimens; all are considered to be paralectotypes, together with the four specimens in the original lot no. 178763, now renumbered as ANSP 398719.

These Schwengel specimens are relatively small, the largest being that one she cited as "Length 11 mm, width 6 mm." In my collection there are several examples that are as much as 14 mm long. Many of the smaller specimens have complete apertures and, assuming that the animal makes the columellar lip only upon maturity (which is by no means certain), there is quite a range of adult size; one paralectotype, for example, has a complete lip but is only 8.8 mm long.

There is also a fair range of width. The lectotype is a relatively narrow shell with a height:width ratio of 2.1:1. The specimen in plate 2, figure 6 has the same proportions as the lectotype; that in figure 8 has a ratio of 1.9:1, and that in figure 7 has a

ratio of 1.8:1. Based on measurement of 30 specimens with complete apertural lips, the species varies from 1.8:1 to 2.1:1, averaging about 2.0:1, with no evident geographic control. In general, it seems that in mature examples (*i.e.*, with complete apertural lips) the smaller examples are more narrow and the larger specimens are less narrow.

At the narrow end of the range *T. didyma* meets the range of specimens of the West African *T. turricula* (von Maltzan, 1884) (pl. 2, figs. 9, 10), which has a height:width ratio ranging from 2.2:1 to 2.4:1. For this reason Houart (1991, p. 33) has placed the two forms in synonymy; however, to me the two completely disjunct averages (2.3 for *T. turricula* and 2.0 for *T. didyma*) indicates that the two should be considered distinct, although closely related, forms.

The widespread occurrences of this species (North Carolina to Venezuela, Brazil from Amapá to Espírito Santo, and off-shore islands) cited by Rios (1970, 1975, 1985, 1994) are complicated by the fact that the species which occurs on the off-shore islands is *T. turricula*, and it is this form that Rios figured in his early works (1975, 1985). However, after Houart (1991, p. 33) stated that the Brazilian species is *T. turricula* and placed *T. didyma* in synonymy, Rios (1994) changed his citation to *T. turricula*. But his illustrated specimen (1994, pl. 37, fig. 475) is *T. didyma* and not *T. turricula,* which is always a more narrow shell (compare pl. 2, figs. 5-10). Along the coast of Sao Paulo, Brazil, in collections made by the Coltro brothers, the form is *T. didyma* (see pl. 2, fig. 7). Therefore, all that can be said at this time is that *T. didyma* apparently occurs along the coast of Brazil, and *T. turricula* occurs on the offshore islands.

De Jong and Coomans (1988) cite *T. didyma* from Curaçao but illustrate only a beautiful SEM picture of the protoconch. Unfortunately, they did not figure their shell but referred to Abbott's (1974, fig. 1873) figure of *Muricopsis withrowi* and to the illustration given in Nowell-Usticke (1959, pl. 3, fig. 14), which is certainly *T. didyma.* However, I have not seen specimens of *T. didyma* from the southern Caribbean. Although the protoconchs of all the species of *Trachypollia* are essentially the same, that of *T. sclera* is slightly more narrow than that of *T. didyma* (compare text-figures 3 and 5), and the illustration given by de Jong and Coomans seems to match *T. sclera* better than *T. didyma.* It is probable that the species they had is not *T. didyma* but *T. sclera.*

Genus LINDAPTERYS Petuch, 1987

Lindapterys PETUCH, 1987, New Caribbean Moll. Faunas, p. 97.

Type species: *Lindapterys vokesae* Petuch, 1987, by original designation.

Discussion: When I originally discussed the generic assignment for an enigmatic shell occuring in the late Early Miocene Chipola Formation of Florida, which I felt to be the same as that one named "*Ranella*" *poppelacki* Hörnes, 1853, from the "Lethyakalk" (middle Miocene) of the Vienna Basin (Vokes, 1974, p. 96), I noted the resemblance to other equally enigmatic species, including the Recent Australian *Daphnellopsis murex* Hedley, 1922, and two French fossil species: *Ranella alata* Millet, 1854, and *Argobuccinum boutillieri* Cossmann, 1889. But, beyond that, I could offer no suggestion for generic placement.

Since that time, we have recognized that *Daphnellopsis,* along with *Phyllocoma* and other two-varixed muricids, properly belongs to the Ergalataxinae. But "*Ranella*" *poppelacki* did not fit into any of the previously known genera. This was resolved by the description of *Lindapterys,* for the Florida and Austrian species, together with a living Caribbean relative, *L. sanderi* Petuch, 1987.

In a subsequent study of the genus *Lindapterys,* both fossil and living, Lozouet *et al.* have determined that the Australian *murex* Hedley is a species of *Lindapterys* (Lozouet *et al.,* 1994, p. 44, pl. 2, figs. 4-6; text-figs. 2C, 2D) and the Late Miocene *alata* Millet is also a *Lindapterys* (*ibid.,* p. 42, pl. 1, figs. 11-16; text-figs. 1C, 1D) but the Middle Eocene *boutillieri* Cossmann is better referred to *Daphnellopsis* (*ibid.,* p. 47, pl. 2, figs. 8, 9). They also figure the holotype of *L. poppelacki* (*ibid.,* p. 42, pl. 1, figs. 9, 10) and two specimens of a form from the

Aquitanian (early Early Miocene) of France, which they identify as *L.* cf. *poppelacki* (*ibid.,* p. 41, pl. 1, figs. 4-8, text-fig. 1A).

Based upon their studies it seems that there are three similar but possibly distinct fossil species (not including *L. alata,* readily distinguished by its cancellate sculpture), which are all in the same lineage *as L. sanderi.* These are:

1) Aquitanian (France) – *L.* cf. *poppelacki,* with multiwhorl (3+ whorls) protoconch, 18-20 axial ribs on body whorl, and a patulous labrum with four denticles;
2) Burdigalian (Florida) – *L. vokesae,* with unknown protoconch (presumed by Lozouet *et al.* to be of the multiwhorl planktotrophic type), about 12 axial ribs on body whorl, and a narrow labrum with five denticles;
3) Badian (Austria) – *L. poppelacki,* protoconch probably multiwhorl (according to Lozouet *et al.*), about 14 axial ribs on body whorl, patulous labrum with five denticles.

The Recent *L. sanderi,* with about 14 axial ribs on the body whorl and a patulous labrum with five denticles, is scarcely distinguishable from the Austrian *L. poppelacki*; however, it has a paucispiral protoconch. As Lozouet *et al.* note, because of the small number of specimens of all of the forms involved, it is preferable not to introduce another name for the Aquitanian form. However, the latter also has a patulous aperture similar to that of *L. poppelacki* and *L. sanderi,* indicating that the living Caribbean species may, in fact, be a descendant of the European side of the line and not the Chipola species.

The only other living species is the western Pacific (Coral Sea) *L. murex,* which has a more cancellate shell ornamentation and elongate outline similar to that of the French *L. alata,* and it is probable that these two represent a species lineage separate from the type species.

LINDAPTERYS VOKESAE Petuch
Plate 3, figure 4

"Ranella" poppelacki Hörnes. VOKES, 1974, Tulane Stud. Geol. Paleont., v. 11, no. 2, p. 96, text-figure 1 (not of Hörnes).
Lindapterys vokesae PETUCH, 1987, New Caribbean Moll. Faunas, p. 98, pl. 15, figs. 10, 11 (after Vokes); LOZOUET *et al.,* 1994, Geobios, no. 27, pt. 1, p. 44, pl. 1, figs. 1-3 (holotype); text-fig. 1B (protoconch).

Description: Dorso-ventrally flattened shell with five teleoconch whorls; protoconch unknown, broken and plugged in unique specimen. Axial ornamention on early teleoconch whorls of 12-14 rounded ribs; on later whorls a flange-like varix developed at random intervals; three on the penultimate whorl, two on the body whorl. Number of intervarical ribs also ran-

PLATE 3

Figures Page

1-3. *Trachypollia trachea* (Gardner) 32
1. (X 6) UF 68774; height 9.0 mm, diameter 4.1 mm.
Locality: UF-WL004, Shoal River, Florida; Shoal River Formation.
2. (X 6) UF 66106; height 8.8 mm, diameter 4.5 mm.
Locality: UF-WL004, Shoal River, Florida; Shoal River Formation.
3. (X 6) UF 68775; height 8.3 mm, diameter 3.8 mm.
Locality: TU 91, Yellow River, Florida; Oak Grove Sand.
4. *Lindapterys vokesae* Petuch 40
(X 5) USNM 647012 (holotype); height 11.7 mm, diameter 5.8 mm.
Locality: TU 951, Tenmile Creek, Florida; Chipola Formation.
5, 6. *Lindapterys sanderi* Petuch 42
5. (X 5) Landau Collection; height 14.5 mm, diameter 6.2 mm.
Locality: TU 1240, Limon, Costa Rica; Moín Formation.
6. (X 5) USNM 859838 (holotype); height 11.6 mm, diameter 6.0 mm.
Locality: Off St. James, Barbados, in 300 meters; Recent.

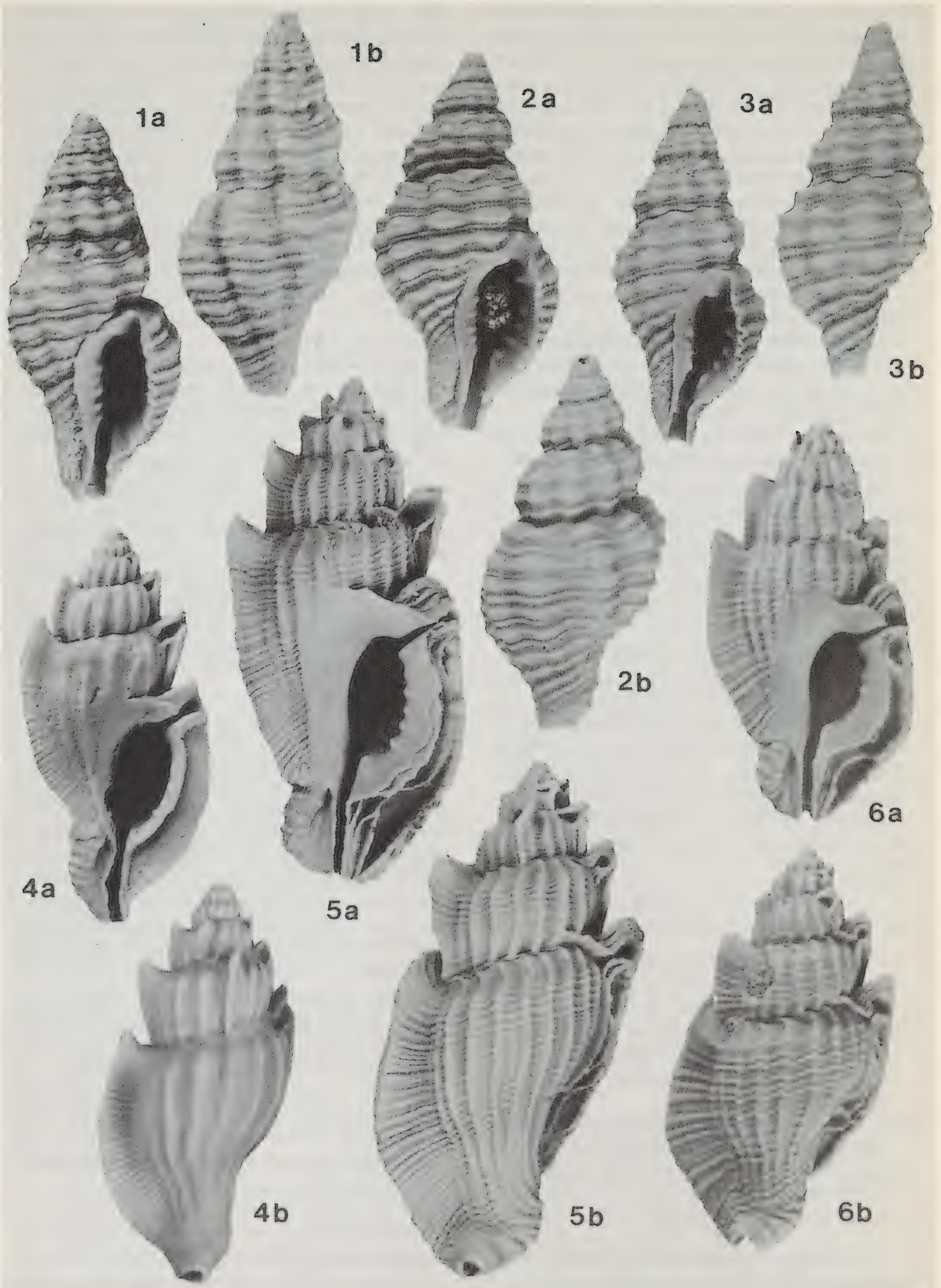


PLATE 3

dom, but the total for each complete whorl approximately 12, interrupted by the varices. Varices wing-like, with an anal channel at the shoulder, opening into the aperture in the manner of *Pterochelus*. Spiral ornamentation of numerous fine threads, with occasional weaker threads intercalated. Suture deeply impressed. Aperture oval, inner lip with a smooth, narrow callus, appressed at posterior end, slightly free-standing at posterior end. Outer lip narrow, with five small denticles on inner side. Siphonal canal short, open, distally recurved.

Holotype: USNM 647012; height 11.7 mm, diameter 5.8 mm.

Type locality: TU 951, Chipola Formation; Ten Mile Creek; south bank, about one and one-quarter miles west of Chipola River (SE 1/4 Sec. 12, T1N, R10W), Calhoun County, Florida.

Occurrence: Chipola Formation, Florida.

Figured specimen: USNM 647012 (holotype).

Discussion: In 1974 I identified a single specimen (which remains unique until today) from the Chipola Formation as the Vienna Basin species *"Ranella" poppelacki* Hörnes, 1853 (see Vokes, 1974, text-figs. 1, 2). With the discovery of a living Caribbean species, Petuch (1987) felt justified in separating the two Miocene forms. Comparison of these two species indicates that *L. poppelacki* is slightly larger than *L. vokesae* with the same number of whorls (both illustrated specimens have five teleoconch whorls); however, the most conspicuous difference is the nature of the aperture, which in *L. poppelacki* is much more expanded and patulous than in *L. vokesae.*

LINDAPTERYS SANDERI Petuch

Plate 3, figures 5, 6

Lindapterys sanderi PETUCH, 1987, New Caribbean Moll. Faunas, p. 98, pl. 15, figs. 5, 6; PETUCH, 1988, Neogene Hist. Trop. Amer. Moll., pl. 38, figs. 13, 14 [not in text]; LOZOUET *et al.,* 1994, Geobios, no. 27, pt. 1, p. 46, pl. 2, figs. 1-3 (holotype); text-figs. 2A, 2B (protoconch).

Lindapterys rosalimae NASCIMENTO DE BARROS, 1990, Siratus, Year 1, no. 2, p. 12 (English), 13 (Portugese), text-figs. 1, 2; LOZOUET *et al.,* 1994, Geobios, no. 27, pt. 1, p. 46, pl. 2, fig. 7 (holotype).

Description: "Shells small for family, dorsoventrally flattened; 2 winglike varices per whorl, with varices aligned up the spire; varices pointed, distinctly channeled; last varix with channel connected to aperture as anal channel; numerous thin, sharp axial ribs between varices, running from suture to siphonal canal; siphonal canal short, open; columellar region with large, adherent parietal shield; outer edge of lip flaring, extending beyond varix; parietal shield and flaring lip producing peristome; inner edge with several denticles; shell sculptured with numerous raised spiral threads; protoconch tiny, similar to genus *Pterochelus*; first postnuclear whorls with several cord-like ribs." (Petuch, 1987, p. 97 – description of *Lindapterys,* new genus)

"General morphology as for genus; 6 axial ribs between varices [6 on ventral side of body whorl, 7 on dorsal side]; 5 labial denticles; outer edge of lip very flaring, almost obscuring the underlying varix." (Petuch, 1987, p. 98)

Holotype: USNM 859838; height 11.5 mm, diameter 6.0 mm.

Type locality: Off St. James, Barbados, in 300 meters.

Occurrence: Moín Formation, Costa Rica; Recent, Barbados to Pernambuco, Brazil.

Figured specimen: Fig. 5, Landau Collection; height 14.5 mm, diameter 6.2 mm; locality TU 1240. Fig. 6, USNM 859838 (holotype).

Discussion: In *L. sanderi,* as Petuch notes in the generic description, the inner and outer lips form a trumpet-like peristome, with the posterior end of the columellar lip appressed to the columellar wall, and the outer lip greatly expanded. This type of aperture differs from the Chipola *L. vokesae,* which has a narrower inner and outer lip; however, it is virtually identical to the Austrian *L. poppelacki* and the French *L.* cf. *poppelacki* (see Lozouet *et al.,* 1994).

Bernard Landau, Albufeira, Portugal, has collected the first known fossil example of *L. sanderi* from the Moín Formation, Costa Rica (pl. 3, fig. 5). This specimen is one-half whorl larger than the holotype, and has eight axial ribs on the ventral side, nine on the dorsal side, suggesting that the number of ribs increases with increasing size.

This is further borne out by a larger Brazilian specimen (height 18 mm) that Nascimento de Barros (1990) named as *L. rosalimae.* This specimen has one more

whorl than the holotype of *L. sanderi* with eight axial ribs between varices on the body whorl, but six on the penultimate, comparable to *L. sanderi*. Although Lozouet *et al.* hesitated to place *L. rosalimae* in the synonymy of *L. sanderi,* as they had not been able to study the unique holotype, I feel no such reluctance.

V. LOCALITY DATA

The following are Tulane University fossil locality numbers:

69. Shoal River Formation, type locality, Shell Bluff, Shoal River (NW 1/4 Sec. 4, T3N, R21W), about 3 1/2 miles north of Mossyhead, Walton Co., Florida.

69A. Shoal River Fm., first ravine upstream from Shell Bluff, Shoal River (NW 1/4 Sec. 4, T3N, R21W), about 3 1/2 miles north of Mossyhead, Walton Co., Florida.

91. Oak Grove Sand, type locality, west bank of Yellow River, about 100 yards below bridge at Oak Grove (NE 1/4 Sec. 20, T5N, R23W), Okaloosa Co., Florida.

705. Bowden Fm., type locality, Bowden, east of Port Morant, Parish of St. Thomas, Jamaica.

951. Chipola Fm., Tenmile Creek, about one and one-quarter miles west of Chipola River (SE 1/4 Sec. 12, T1N, R10W), Calhoun Co., Florida.

1240. Moín Fm., Barrio Los Corales, top of hill at end of road that passes Standard Fruit Company box factory, 1.8 km north of main highway at Pueblo Nuevo, which is 2 km west of Puerto Limon, Costa Rica.

The following is a Florida Museum of Natural History fossil locality number:

UF-WL004. Shoal River Fm., Shoal River (NW 1/4 Sec. 4, T3N, R21W), about 3 1/2 miles north of Mossyhead, Walton Co., Florida (? = TU 69A).

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THE GENUS *PHALIUM* (GASTROPODA: CASSIDAE) FROM THE ALUM BLUFF GROUP OF NORTHWESTERN FLORIDA

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The purpose of this paper is to reexamine the genus *Phalium* from the Alum Bluff Group of northwestern Florida. Over a century has elapsed since Dall first described a single specimen of this genus from Chipola Formation deposits. His new species was collected from Ten Mile Creek in Calhoun County, Florida, and given the name *Phalium aldrichi* to honor Mr. T.H. Aldrich, who was instrumental in furthering our knowledge of the Eocene fauna of the southern United States (Gardner, 1947, p. 537). Since this initial discovery, numerous specimens of *Phalium* have been collected by professional and amateur fossil hunters from the late Early Miocene Chipola deposits along Farley Creek, the Chipola River, and Tenmile Creek. In addition, one complete, as well as many partial specimens of *Phalium* have been unearthed from the Middle Miocene Shoal River Formation.

The newly collected Chipola Formation examples of *Phalium* exhibit a wide range of morphological forms and the single complete *Phalium* from the Shoal River deposit bears a strong resemblance to one of the Chipola varieties. These discoveries posed two questions to the investigator. First, does the Chipola Formation possess more than one species of *Phalium*, or do the different varieties of *Phalium* simply represent different forms of *Phalium aldrichi*? Second, does the *Phalium* from the Shoal River deposit represent a new species, or is it a form of *Phalium aldrichi* that survived into the Middle Miocene?

To answer the first question the investigator examined 30 specimens of *Phalium* collected from eight different Chipola Formation localities. Pictures were taken of the different morphological types (pl. 1, figs. 1-5), and the protoconchs of three different forms were examined with the help of SEM photographs (pl. 2). Although none of the specimens examined look exactly like the holotype described by Dall (1890, p. 162), the specimen illustrated in plate 1, fig. 1, has all of its morphological characteristics with the exception of the two prominent transverse varices. An examination of the pictured specimens of Chipola *Phalium* illustrates a gradual transition in form from Dall's shouldered variety, with distinct nodes on the periphery of the body and penultimate whorls, to a rounded, more cancellate form. In addition, a comparison of the SEM photographs of the protoconchs and early teleoconch whorls of the shouldered forms (pl. 2, figs. 1 and 2) with the rounded, more cancellate variety (pl. 2, fig. 3) reveals that the protoconchs and early sculpturing on the teleoconch whorls are exactly the same for all varieties. This evidence strongly suggests that *Phalium aldrichi* is the only species of *Phalium* present in Chipola Formation deposits, and that like other members of its genus, *Phalium aldrichi* reflects a high degree of morphological variability.

The complete *Phalium* collected from Shoal River deposits (pl. 3, fig. 1) may be compared visually to its closest Chipola counterpart in plate 3, fig. 2. Although the two specimens appear to be the same, the Shoal River species is a much larger and more globose shell, which possesses different sculpturing on the body and teleoconch whorls. These differences have led the investigator to conclude that the Shoal River specimen represents a new species that evolved from *Phalium aldrichi.*

SYSTEMATIC PALEONTOLOGY

Family CASSIDAE Swainson, 1832
Genus PHALIUM Link

Phalium LINK, 1807, Beschr. Natur.-Samm. Univ. Rostock, p. 112.

Type species: *Buccinum glaucum* Linné, 1758, by subsequent designation, Dall (1909, U.S. Geol. Survey, Prof. Paper 59, p. 62).

Subgenus TYLOCASSIS Woodring

Tylocassis WOODRING, 1928, Carnegie Inst. Washington, Publ. 385, p. 306.

Type species: *Buccinum granulatum* Born, 1780, by original designation.

PHALIUM (TYLOCASSIS) MURRAYI
Schmelz, n. sp.
Plate 3, figure 1

Description: Shell medium-sized, thin, globose. Protoconch smooth, glossy, about three whorls, becoming abruptly sculptured with faint spiral cords and axial ridges. Four and one-half teleoconch whorls. Early whorls strongly convex, last two whorls more flattened. Suture distinct. Penultimate whorl sculptured with four alternating narrow and wide spiral cords, intersected by faint axial ridges. Intersected cords faintly crenulate. Crenulations best developed along the shoulder where they give the shell a weakly tuberculate appearance. Body whorl with 13 broad, slightly raised cords separated by narrow, smooth spaces. Outer lip thickened, reflected, with outer edge coarsely crenulated. Nineteen, well-developed, unpaired lirae situated along the inside edge of the outer lip. Inner lip heavily calloused, reflected, pustular, lirate along the inside edge. Siphonal canal short, strongly recurved; siphonal fasciole well-developed and situated next to a deep groove.

Holotype: UF 67410; height 45.5 mm, maximum diameter 33.5 mm.

Type locality: WL004, Shoal River Formation, New Harmony Quadrangle USGS 1987, (Sec. 4, T3N, R21W), Walton County, Florida.

Etymology: Named for Andrew Murray, who collected the type specimen, now in the collection of the Florida Museum of Natural History.

Discussion: The most recent strontium dating studies on the Shoal River Formation show that these deposits are about 4.5 to 8.5 million years younger than their Chipola Formation counterpart (Jones *et al.,* 1993, tbl. 1, p. 45). In addition, fossils collected from this deposit suggest that the climate was cooler and the reef environment of the Chipola Formation had been replaced by a shallow-water, silty bottom (Gardner, 1926, p. 2; Hoerle, 1976, p. 3). Under these new environmental conditions, *Phalium aldrichi* evolved into the larger, more globose *Phalium murrayi.* Like its Chipola counterpart, fragments of *Phalium murrayi* collected by the investigator indicate that the new species had a wide range of morphological forms with some possessing smooth body whorls and noded shoulders, while others lack the noded shoulders and have cancellate sculpturing.

Phalium murrayi is considered to be the ancestor to *Phalium reclusa* (Guppy, 1873), which is reported from the Late Miocene-Pliocene Cercado and Gurabo formations of the Dominican Republic (Woodring, 1928, p. 308), the Late Miocene Gatun Formation of the Panama Canal Zone (Woodring, 1959, p. 200, pl. 34, figs. 1, 4-6) and the Late Pliocene deposits of the Bowden formation in Jamaica (Guppy, 1866, p. 287, pl. 17, fig. 8; Woodring, 1928, p. 307, pls. 19, 20). For comparative purposes two typical forms of *Phalium reclusa* from two different Dominican Republic localities are pictured in Plate 3. The smaller, cancellate form (fig. 3) comes from the Cercado formation on the Rio Cana at Caimito (TU 1230) and the larger specimen (fig. 4), with the double row of nodes at the shoulder, comes from Cercado Formation deposits on the Rio Gurabo (TU 1358). *Phalium murrayi* bears the closest resemblance to the specimen of *Phalium reclusa* illustrated in figure 4. Both are about the same size, but *Phalium murrayi* is more globose, lacks the double row of nodes at the shoulder, has early teleoconch whorls that are more convex, and possesses a more elevated protoconch with three rather than two and one-half whorls.

PLATE 1

Figures
1-5. Different morphological types of *Phalium aldrichi* Dall, from the Chipola Formation, Florida. (All X 1´)

1. UF 68995; height 32.5 mm, diameter 21.2 mm; locality TU 951.
2. UF 68996; height 35.9 mm, diameter 28.4 mm; locality TU 655.
3. UF 68997; height 32.2 mm, diameter 21.0 mm; locality TU 655.
4. UF 68998; height 37.8 mm, diameter 23.7 mm; locality TU 951.
5. UF 68999; height 35.6 mm, diameter 27.3 mm; locality TU 825.

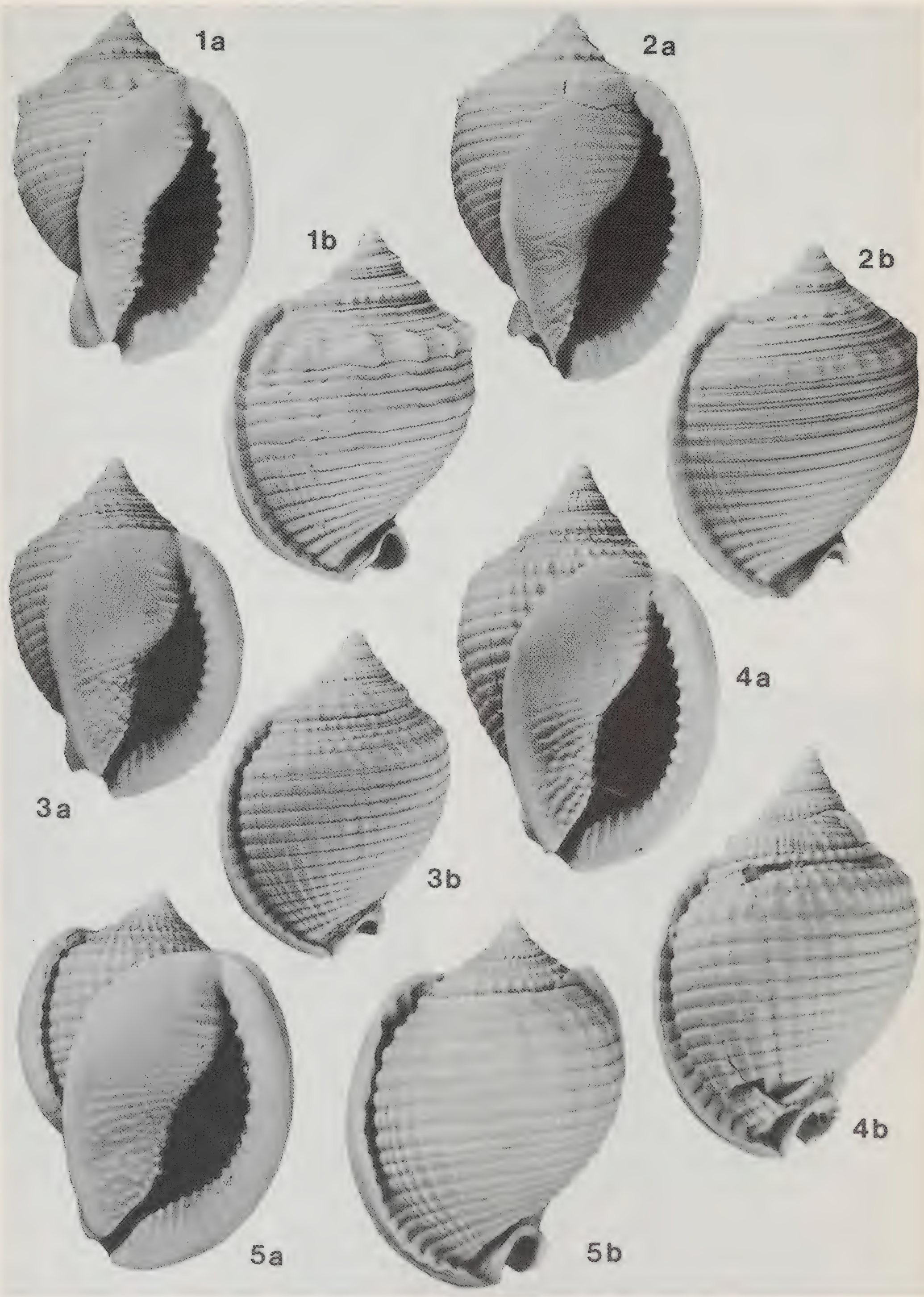

PLATE 1

A number of other Late Miocene and Pliocene species of *Phalium* have been described from Florida, the Caribbean, and South America. These include *Phalium moniliferum* (Guppy, 1866) (see Maury, 1917, p. 110, pl. 44, figs. 4-5) from the Dominican Republic, *Phalium (Tylocassis) sulcosum* var. *senni* (Rutsch, 1934, p. 55, pl. 3) from Venezuela, *Semicassis (Tylocassis) inflata waltonensis* (Mansfield, 1935, p. 40, pl. 4, figs. 5, 9) from Florida, and *Semicassis (Tylocassis) maleaformis* (Vokes, 1938, p. 24, figs. 22-23) from Trinidad. In general, these species are morphologically very similar to *Phalium reclusa* and are considered synonyms of that species by Abbott (1968, p. 163). In addition, Maury (1925, p. 199, pl. 5, figs. 5-7) collected a unique high spired species, *Phalium paraensis,* from Early Miocene, Pirabas Formation, deposits in Brazil. This species may predate *Phalium aldrichi,* but additional geologic dating needs to be done on this formation in order to confirm its appropriate evolutionary placement (Vokes, personal communication).

Pilsbry (1922, p. 361) suggested that *Phalium reclusa* is the ancestor to both *Phalium granulatum* (Born, 1778) in the Atlantic and *Phalium centiquadrata* (Valenciennies, 1832) in the Pacific. This investigator has discovered numerous fossil specimens of *Phalium granulatum* in Florida Pleistocene deposits at the Capeletti Brothers pit in Dade County, and the Griffin Brothers quarry in Palm Beach County. *Phalium granulatum* was also collected from Florida Plio-Pleistocene spoil piles at Star Ranch in Palm Beach County. An examination of over a hundred specimens of *Phalium granulatum* from these locations reveals that they possess a wide range of morphological forms, some of which are identical to *Phalium alligator* (Petuch, 1991, p. 23, pl. 3, figs. 13-14), and *Phalium granulatum loxahatcheensis* (Petuch, 1994, p. 272, pl. 38, figs. A-B). These findings suggest that both *Phalium alligator* and *Phalium granulatum loxahatcheensis* should be considered synonyms for *Phalium granulatum. Phalium cicatricosum* (Gmelin, 1791) cited by Petuch (1994, p. 188, pl. 38, fig. F) for a fossil from the Capeletti Brothers pit, is listed by Abbott (1968, p. 157) as a synonym of *Phalium granulatum.*

This investigator would like to extend a special note of thanks to Emily Vokes for the loan of Tulane specimens and her assistance with photographic work. Zuzana Hruska, Coordinated Instrumentation Facility, Tulane University, provided the SEM protographs. Additional notes of appreciation are extended to Mr. Burt Hayes and Mr. Cecil Sexton for granting permission to collect on their property, to Roger Portell, Florida Museum of Natural History, Gainesville, for reviewing the article, and to Andrew and Greta Murray, Bradenton, Florida, for their donation of specimens.

LOCALITY DATA

The following are Tulane University fossil locality numbers:

655. Chipola Fm., Tenmile Creek, about 0.1 mile downstream from bridge of Florida Highway 73 (NW 1/4 Sec. 12, T1N, R10W), Calhoun Co., Florida.
825. Chipola Fm., Farley Creek at abandoned mill about 1/4 mile west of bridge of Florida Highway 275 (SW 1/4 Sec. 21, T1N, R9W), Calhoun Co., Florida.
951. Chipola Fm., Tenmile Creek, about 1/4 mile west of Chipola River (SE 1/4 Sec. 12, T1N, R10W), Calhoun Co., Florida.

PLATE 2

Figures
1-3. SEM photographs of different morphological types of *Phalium aldrichi* Dall, from the Chipola Formation, Florida. (X 20)

1. UF 68995; height 32.5 mm, diameter 21.2 mm; locality TU 951.
2. UF 68996; height 35.9 mm, diameter 28.4 mm; locality TU 655.
3. UF 68999; height 35.6 mm, diameter 27.3 mm; locality TU 825.

1

2

3

PLATE 2

1230. Cercado Fm., Rio Cana, east bank, just above bridge at Caimito on Los Quemados - Sabaneta Road, Dominican Republic.
1358. Cercado Fm., Rio Gurabo, west side and downstream from mouth of Arroyo La Cabra, approximately 6 km (airline) above the ford on Los Quemados-Sabaneta Road, Dominican Republic.

The following is a Florida Museum of Natural History fossil locality number:

WL004. Shoal River Fm., New Harmony Quadrangle USGS 1987 (Sec. 4, T3N, R21W), Walton Co., Florida.

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PLATE 3

Figures
1-4. A comparison of *Phalium murrayi* with *Phalium aldrichi* Dall and *Phalium reclusa* (Guppy). (All X 1 1/2)

1. *Phalium murrayi* Schmelz, n. sp.
   UF 67410 (holotype); height 45.5 mm, diameter 33.5 mm.
   Locality: WL004, Shoal River Formation, Walton County, Florida.
2. *Phalium aldrichi* Dall
   UF 68995; height 32.5 mm, diameter 21.2 mm.
   Locality: TU 951, Chipola Formation, Florida.
3. *Phalium reclusa* (Guppy)
   UF 70000; height 26.6 mm, diameter 18.2 mm.
   Locality: TU 1230, Cercado Formation, Rio Cana at Caimito, Dominican Republic.
4. *Phalium reclusa* (Guppy)
   UF 68993; height 45.8 mm, diameter 30.6 mm.
   Locality: TU 1358, Cercado Formation, Rio Gurabo, Dominican Republic.

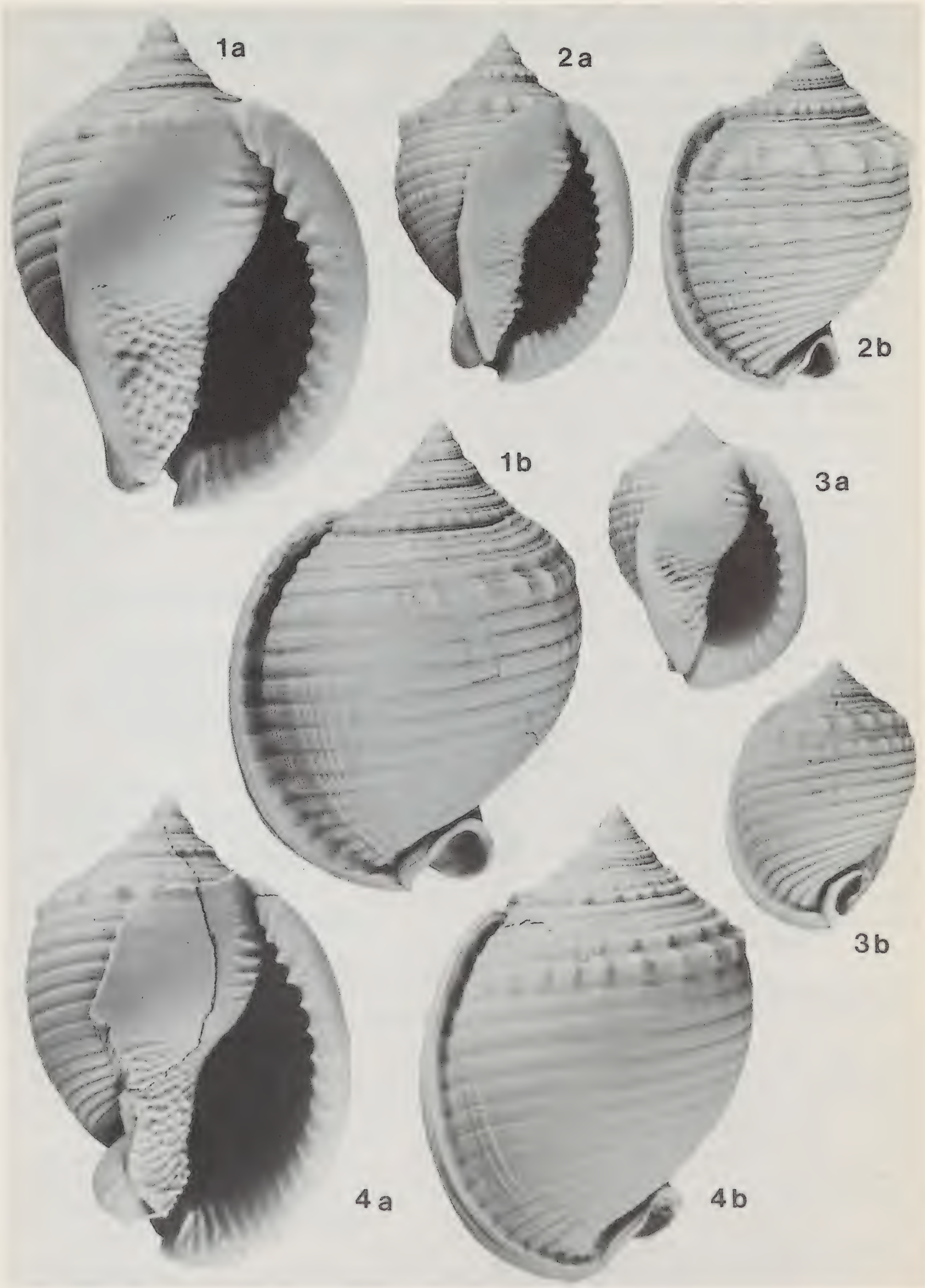

PLATE 3

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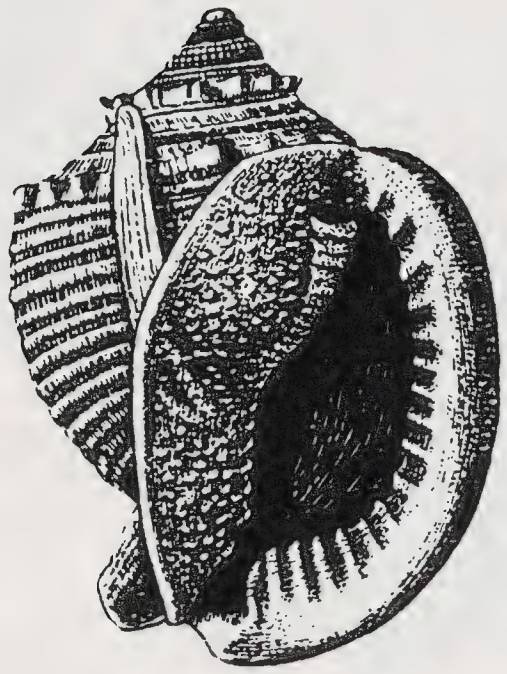

A NEW SPECIES OF *MORUM* (GASTROPODA: HARPIDAE) FROM THE LOWER MIOCENE CANTAURE FORMATION OF VENEZUELA

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The Cantaure Formation is exposed in a series of arroyos about 500 meters south of an abandoned house known as "Casa Cantaure," which is 14 km west of the village of Pueblo Nuevo in the Paraguaná Peninsula, Venezuela. Since the Cantaure Formation was first monographed by Jung (1965), a trickle of new species have been described in the literature thanks to collecting done in the 1970's by Mr. and Mrs. Jack Gibson Smith, then of Caracas, now of Surrey, England. My interest aroused by their reports, I visited the locality in 1992 and returned in 1995. My own collecting produced numerous new and unusual shells, one of which is described here.

SYSTEMATIC PALEONTOLOGY

Class GASTROPODA
Order NEOGASTROPODA
Superfamily VOLUTOIDEA
Family HARPIDAE Bronn, 1849
Genus MORUM Röding

Morum 'BOLTEN' RÖDING, 1798, Mus. Boltenianum, pt. 2, p. 53.

Type species: *Morum purpureum* Röding, 1798 [= *Strombus oniscus* Linnaeus, 1767], by monotypy.

Subgenus ONISCIDIA Mörch

Oniscidia MÖRCH, 1852, Cat. Conch. Yoldi, pt. 1, p. 111.

Type species: *Oniscia cancellatum* Sowerby, 1824, by monotypy.

MORUM (ONISCIDIA) JUNGI
Landau, n. sp.
Plate 1, figures 1, 2

Description: Shell small for subgenus, solid, barrel-shaped, reaching a maximum height of about 30 mm and diameter about 20 mm; body whorl large, forming five-sixths of the total height, with a small scalate spire. Protoconch turbinate, smooth, consisting of about one and one-quarter whorls. Five postnuclear whorls with a sharply angled peripheral shoulder just below a well-defined suture. Space above shoulder wide. Body whorl rapidly constricting about two-thirds of the distance from suture, forming well-defined, posteriorly-twisting, anterior canal. Sculpture of body whorl above shoulder consisting of strong axial ribs with a roughly concave area between them, crossed by numerous axial incremental threads; spiral sculpture very weak, two spiral cords bearly discernable. Sculpture below shoulder cancellated by eleven sharp, narrow axial ribs, free edges fluted by spirals; in later whorls distinctly laminated, rising at shoulder to form sharp points. Incrementals between axial ribs numerous, appearing as thin threads. Nine well-rounded, spiral cords, subequal and regularly spaced. Spirals separated by concave interspaces about twice width of cords. Aperture almost as long as body whorl, nearly elliptical in form, outer lip thickened by a raised rib and denticulated along inner margin. Parietal callus wide, reflected onto body wall and siphonal canal, edge free. Surface of callus coarsely granulated, granulations irregular but tending to be elongated and oriented normal to axis along oblique inner margin of aperture. Siphonal canal broad and well demarcated, twisting posteriorly.

Holotype: Naturhistorisches Museum Basel H 17763; height 26.5 mm, diameter 18.0 mm (Plate 1, fig. 1).

Type locality: NMB 17516, Cantaure Formation; series of arroyos about 500 meters south of "Casa Cantaure," which is 14 km (by road) west of Pueblo Nuevo, Paraguaná Peninsula, Falcón, Venezuela.

Paratype: Naturhistorisches Museum Basel H 17764; height 24.2 mm, diameter 15.8 mm (Plate 1, fig. 2).

Unfigured paratype 1: Bernard Landau collection; height 29.5 mm, diameter 19.5 mm.

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Unfigured paratype 2: Bernard Landau collection; height 25 mm, diameter 17 mm.

Locality of all, same as holotype.

Etymology: named for Peter Jung of the Naturhistorisches Museum, Basel, Switzerland, in recognition of his work on the Cantaure Formation.

Discussion: Morum (Oniscidia) jungi is a rare species in the Cantaure Formation. Four type specimens are known, two at the Naturhistorisches Museum Basel and two in my personal collection. Five additional specimens were collected by Mr. and Mrs. Jack Gibson Smith and donated to the Basel Museum (Peter Jung, pers. comm.).

The new species is most closely related to *Morum (Oniscidia) chipolanum* Dall *in* Maury, 1925, from the Chipola Formation of northern Florida, but differs from that species in being smaller with a squatter, broader outline, having a more constricted body whorl, fewer axial ribs (11 as opposed to 15 in *M. chipolanum*) and more numerous, weaker denticles on the inner aspect of the outer lip, which do not correspond to the spiral cords as they do in *M. chipolanum* (compare pl. 1, figs. 1, 3).

Morum (Oniscidia) jungi, by its cancellate sculpture, also resembles the chronologically younger *M. domingense* (Sowerby, 1850), from the Cercado and Gurabo formations (Mio-Pliocene) of the Dominican Republic. The Dominican species has a narrow, well-defined sulcus at the posterior commisure absent in *M. jungi.* This has led to its placement in the subgenus *Herculea* by various authors; however, as pointed out by Beu (1976, p. 224), the deep posterior sulcus is not a consistent distinguishing feature for the subgenus *Herculea* and it is better placed within the subgenus *Oniscidia* by virtue of its strongly cancellate sculpture. *Morum jungi* is also smaller and less elongated than *M. domingense* with a lesser number of spiral cords and axial ribs (compare pl. 1, figs. 1, 4).

I would like to thank Emily Vokes, Tulane University, Louisiana, for her help and encouragement.

LOCALITY DATA

The following are Tulane University fossil locality numbers:

554. Chipola Fm., east bank of Chipola River at power line crossing (SW 1/4 Sec. 17, T1N, R9W), Calhoun Co., Florida.

1215. Gurabo Fm., Rio Gurabo, bluffs on both sides, from the ford on Los Quemados-Sabaneta road, upstream to approximately 1 km above the ford, Dominican Republic.

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PLATE 1

Figures

1-2. *Morum (Oniscidia) jungi* Landau, n. sp.
   1. (x 2.5) NMB H 17763 (holotype); height 26.5 mm, diameter 18 mm.
   2. (x 2.5) NMB H 17764 (paratype); height 24.2 mm, diameter 15.8 mm.
   Locality of both: NMB 17516, Paraguaná Peninsula, Venezuela; Cantaure Formation.

3. *Morum (Oniscidia) chipolanum* Dall *in* Maury
   (x 2) PRI 45248; height 25.4 mm, diameter 17.6 mm.
   Locality: TU 554, Chipola River, Florida; Chipola Formation.

4. *Morum (Oniscidia) domingense* (Sowerby)
   (x 1.5) PRI 45254; height 33.0 mm, diameter 20.7 mm.
   Locality: TU 1215, Gurabo River, Dominican Republic; Gurabo Formation.

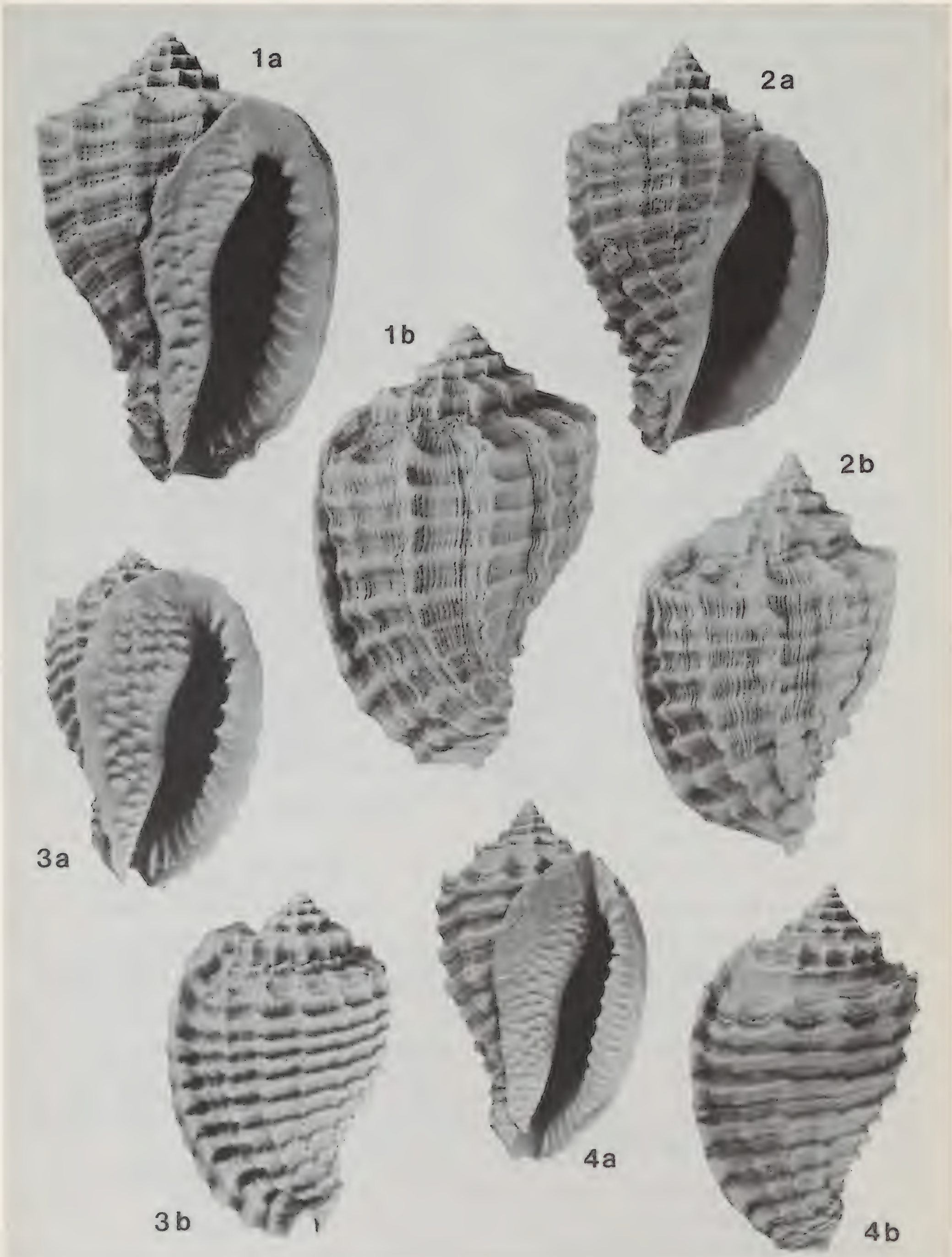

PLATE 1

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July 31, 1996

A NEW SPECIES OF *MANSFIELDELLA* (GASTROPODA: OLIVIDAE: OLIVELLINAE) FROM THE PLEISTOCENE BERMONT FORMATION OF SOUTHERN FLORIDA

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Mansfieldella, an olivelline gastropod genus, was erected by Olsson and Harbison (1953, p. 188). It is distinguished from other genera within the Olivellinae by a heavily developed parietal callus, which spreads thickly over the surface of the spire-whorls covering the sutures except the final half of the last whorl, and a strongly lirate pillar structure in which the anterior and posterior lirations are enlarged and tooth-like. Until now the genus included a single species, *Olivella (Mansfieldella) pugilis*, described by the authors in the same work. *Mansfieldella pugilis,* a relatively common and distinctive shell, was originally described from the Pliocene of St. Petersburg and is common in the Pliocene Pinecrest Beds at Sarasota, Florida.

During a field trip in November, 1992, to Palm Beach County, Florida, Palm Beach Rock Co. quarry was visited on several occasions. The quarry is situated on the north side of U.S. Highway 441, three miles west of Loxahatchee. Most of the quarried rock consists of whitish coral and coral rubble with sands rich in molluscs. The shell assemblage is Bermont Formation, characterised by *Strombus evergladesensis* Petuch, 1991, *Jenneria loxahatchiensis* M. Smith, 1936, and *Zonaria (Prozonaria) portelli* (Petuch, 1990). In the centre of the quarry were a few mounds of finer grey sands, dredged from below the coral-rich layer. Within these sands were large numbers of *Mansfieldella robbieae,* n. sp., in association with *Niveria pediculus pediculus* (Linné, 1758) and *Nitidella nitida* (Lamarck, 1822).

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SYSTEMATIC PALEONTOLOGY

Class GASTROPODA
Order NEOGASTROPODA
Superfamily VOLUTOIDEA
Family OLIVIDAE
Subfamily OLIVELLINAE
Genus MANSFIELDELLA Olsson and Harbison, 1953

Mansfieldella OLSSON and HARBISON, 1953, Acad. Nat. Sci. Phila., Mon. 8, p. 188.
Type species: *Olivella (Mansfieldella) pugilis* Olsson and Harbison, by original designation.

MANSFIELDELLA ROBBIAE
Landau, n.sp.
Plate 1, figures 1-3

Mansfieldella cf. *pugilis* (Olsson and Harbison). PETUCH, 1994, Atlas of Florida Fossil Shells, pl. 84, fig. E.

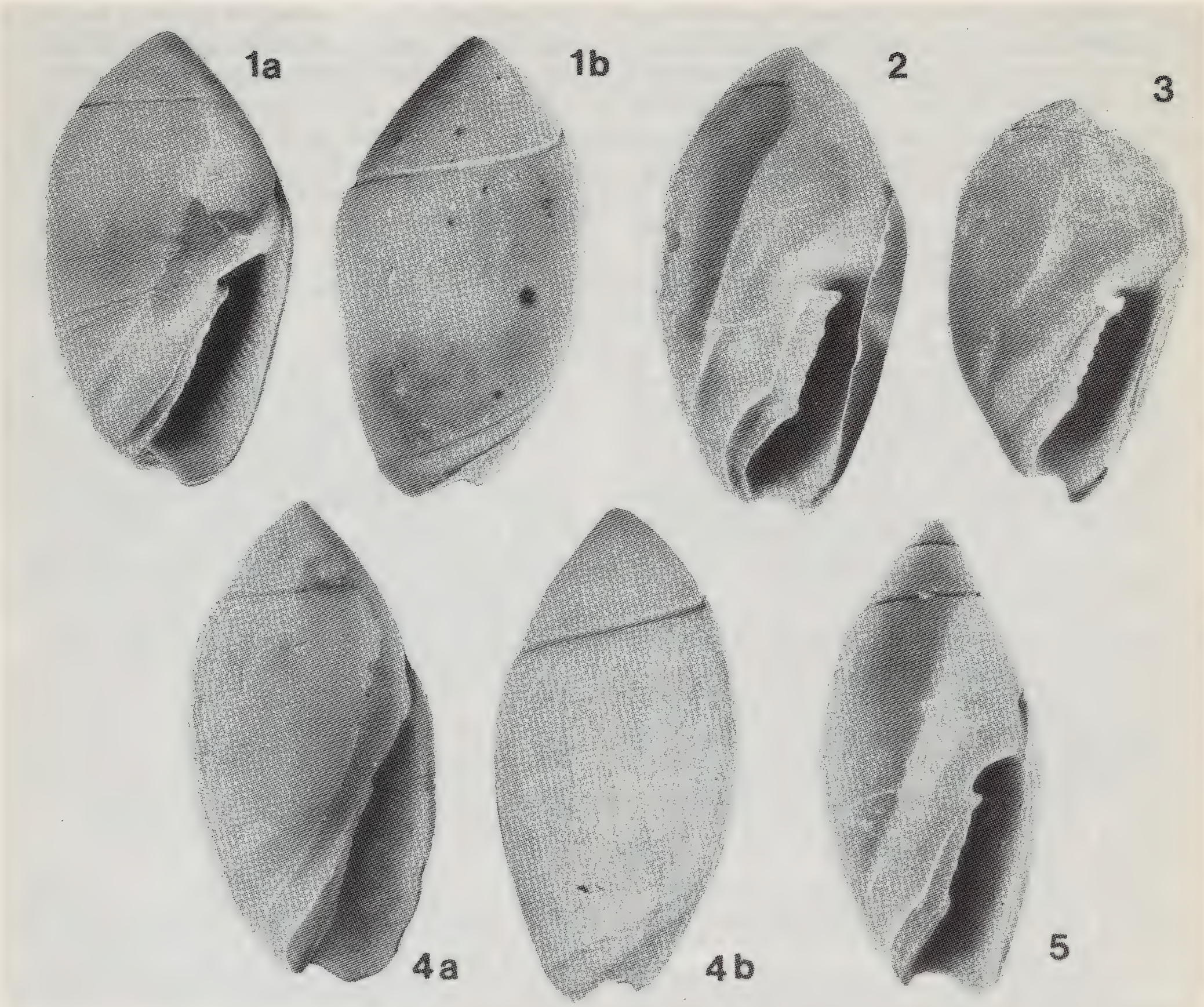

PLATE 1

1-3. *Mansfieldella robbieae* Landau, n. sp.
1. (X 6) UF 71296 (holotype); height 8.0 mm, diameter 4.7 mm.
2. (X 6) UF 71297 (paratype A); height 8.1 mm, diameter 4.7 mm.
3. (X 6) UF 71298 (paratype B); height 7.3 mm, diameter 4.6 mm.
Locality of all: Palm Beach Rock Co. quarry, Palm Beach County, Florida; Bermont Formation.

4-5. *Mansfieldella pugilis* Olsson and Harbison, 1953
4. (X 5) UF 71299; height 11.2 mm, diameter 6.0 mm.
Locality: TU 769, Kissimmee River, Florida; Pinecrest Formation.
5. (X 6) UF 71300; height 8.3 mm, diameter 4.0 mm.
Locality: TU 1000, Sarasota, Florida; Pinecrest Formation.

Description: Shell small, squat, reaching a maximum height of about 8 mm and diameter about 4.5 mm, oval in outline, solid. Shell spire low, about one fifth total height, apex rounded with a small pointed tip visible in less strongly callused specimens. Protoconch, spire whorls, and sutures obscured by callus. Deep groove-like suture between body whorl and spire. Body whorl sub-cylindrical, antero-posteriorly flattened, contracted in zone of fasciolar band. Parietal callus strong, thickest opposite apical end of aperture and from there spreading upwards to tip of apex. Pillar structure a raised plate or shelf carrying a strong fold below, rotating outward, with a sharp tooth at apical end. Between these three to six smaller lirations of variable strength. Outer lip not thickened, internally with long lirations opposite those of the pillar structure. Surface smooth and polished.

Holotype: UF 71296; height 8.0 mm, diameter 4.7 mm (Plate 1, fig. 1).

Type locality: Palm Beach Rock Co. quarry north side of U.S Highway 441, three miles west of Loxahatchee, Palm Beach County, Florida.

Paratype A: UF 71297; height 8.1 mm, diameter 4.7 mm; locality, Palm Beach Rock Co. quarry (Plate 1, fig. 2).

Paratype B: UF 71298; height 7.3 mm, diameter 4.6 mm; locality, Palm Beach Rock Co. quarry (Plate 1, fig. 3).

Occurrence: Bermont Formation, southern Florida; Pleistocene.

Etymology: named after Dr. Sheila Robbie of the University of the Algarve, Portugal, Professor of Languages and amateur fossil enthusiast, who first collected this small shell.

Discussion: Specimens of *Mansfieldella robbiae* were first collected by Dr. Robbie and myself in 1992 and donated for description to Dr. Edward Petuch of Florida Atlantic University. In his recent monograph on the fossil shells of Florida (1994, pl. 84, fig. E) he has figured the specimen donated as *M.* cf. *pugilis.* This unusual little shell, being only the second member of the genus *Mansfieldella,* deserves more attention.

The new species, although obviously closely related to *M. pugilis* (pl. 1, figs. 4, 5) and probably descended from it before the genus became extinct, can be distinguished from its Pliocene predecessor at a glance by the oval shape and rounded spire, as opposed to *M. pugilis,* which is bullet-shaped with a pointed spire. The sutures on the spire whorls, which are visible in *M. pugilis,* except where they are covered by the upwards spreading parietal callus, are completely obscured by callus in *M. robbiae.*

There seems little variation between the specimens of *M. robbiae.* The size and shape is constant with some variation in the number and strength of the lirations on both the inner and outer lips. In the younger, less callused specimens, in which there is a pointed mammilation at the tip of the apex this has some remnants of orangy-brown pigmentation. The shell has only been found at Palm Beach Rock Co. quarry where it is abundant in the sandy facies.

LOCALITY DATA

The following are Tulane University fossil locality numbers:

769. Pinecrest beds, spoil banks east side of Kissimmee River, 1 1/2 to 2 miles south of U.S. Corps of Engineers Structure 65-D (NE 1/4 Sec. 35, T36S, R33E), Okeechobee Co., Florida.

1000. Pinecrest beds, APAC pits at east end of 17th Street (T36S, R19E), about 8 miles east of U.S. Highway 301 at Sarasota [now north west corner of Fruitville exit, I-75], Sarasota Co., Florida.

LITERATURE CITED

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PETUCH, E. J., 1994, Atlas of Florida fossil shells (Pliocene and Pleistocene marine gastropods). Chicago Spectrum Press, Evanston, Illinois, 394 p., 100 pls., 20 text-figs.

July 31, 1996

A NEW SPECIES OF *RHYNCHOLAMPAS* (ECHINOIDEA: CASSIDULIDAE) FROM THE CHIPOLA FORMATION: THE FIRST CONFIRMED MEMBER OF THE GENUS FROM THE MIOCENE OF THE SOUTHEASTERN U.S.A. AND THE CARIBBEAN

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The cosmopolitan echinoid genus *Rhyncholampas* is found in deposits ranging from the Paleocene to the Recent. In the southeastern United States and the Caribbean, the genus is a common constituent of Eocene, Oligocene and Pliocene-Pleistocene strata. Three different species of *Rhyncholampas* have been reported from "Miocene" units in Florida, North and South Carolina, and Cuba over the last seventy years. However, no verifiable records of the genus as occurring in the Miocene of the southeastern United States or the Caribbean can be substantiated.

Revisions in paleontologic taxonomy and stratigraphic age interpretations for *Rhyncholampas* species require a new interpretation for the history of this echinoid genus. Sanchez Roig (1926) first reported the species description and geologic age for *Rhyncholampas rodriguezi* Lambert and Sanchez Roig, 1926, as a new taxon from the lower Oligocene of Cuba. In the same monograph, Sanchez Roig reported collecting specimens he referred to as *Rhyncholampas* sp. cf. *R. alabamensis* (a species in the genus *Cassidulus*), from a lower Oligocene unit as well. More than twenty years later, Sanchez Roig (1949) listed both taxa as occurring in Tertiary rocks in Cuba, but altered his original interpretation for the ages of the stratigraphic units from which these two species were collected. He indicated the formation containing *R. rodriguezi* was a lower Miocene unit and the formation containing *Rhyncholampas* sp. cf. *R. alabamensis* potentially was an Oligo-Miocene unit (rather than Oligocene as previously had been proposed for both taxa).

More recently, Kier and Lawson (1978) compiled an index of living and fossil echinoids from papers published prior to 1971, and included *R. rodriguezi* as part of lower Oligocene stratigraphic units only, not the Miocene as reported by Sanchez Roig. Kier (1984) briefly addressed the stratigraphic age problem of several echinoids previously reported from Cuba, and the uncertainty of the stratigraphic units' status and potential correlation to units in the United States. During this discussion, the list of echinoid taxa provided by Kier did not specifically pertain to cassiduloids (and therefore did not include any species of *Rhyncholampas*). It is of relevance to this paper, however, because he stated that several of the stratigraphic distribution reports for the Miocene echinoids should be used with caution when trying to correlate stratigraphic units in Cuba to regions outside the island. The second potential Miocene echinoid from Cuba, listed by Sanchez Roig (1926) as *Rhyncholampas* sp. cf. *R. alabamensis*, no longer is of concern either, since Cooke (1959) synonomized *Cassidulus alabamensis* with *Rhyncholampas gouldii* (Bouve, 1846), which has been reported only from Oligocene strata.

The third species of echinoid of significance to this paper was reported from the Miocene in Florida. Cooke (1959) reported *Cassidulus sabistonensis* Kellum, 1931, present in the late Miocene Tamiami Formation of Florida as well as localities in North and South Carolina. Kier (1962) did not formally place this species in the *Rhyncholampas* genus in his monograph, but strongly suggested a detailed analysis would warrant a revision from its position within the *Cassidulus* genus as Cooke (1959) proposed. Regardless of the taxonomic status of the echinoid, the stratigraphic age of the Tamiami Formation is no longer interpreted to be Miocene as Cooke reported in his monograph. The age of the Tamiami Formation in Florida presently is considered to be Pliocene (see the details in the discussion section) and therefore, this echinoid would not repre-

sent a Miocene record of the genus *Rhyncholampas*.

In 1993, a single, fairly well-preserved specimen of *Rhyncholampas* was found in early Miocene Chipola Formation sediment by Andrew and Greta Murray while snorkeling along the Chipola River in Calhoun County, Florida. This specimen, named *Rhyncholampas chipolanus,* n. sp., herein represents the first record of the genus from the Miocene of Florida, as well as the rest of the southeastern United States and Caribbean.

The Murrays collected the specimen at UF locality CA025, *in situ,* from one meter below the top of the Chipola Formation shell bed. At the site, Chipola strata is known to be at least 2.5 meters thick and consists of a loose, fine- to coarse-grained, quartz sand with limy boulders, coral head fragments, and numerous mollusk shells.

Taxa collected in association with the Chipola *Rhyncholampas* include test fragments and spines of the echinoid *Prionocidaris cookei* Cutress, 1976, *Clypeaster concavus* Cotteau, 1875, and an unconfirmed species of *Abertella* (see Cooke, 1959, p. 45). Numerous mollusks also are common, including the gastropods *Rhinoclavis chipolana* (Dall, 1892), *Terebralia dentilabris* (Gabb, 1873), *Tenuicerithium chipolanum* (Dall, 1892), *Orthaulax gabbi* Dall, 1890; and the bivalves *Donax trueloides* Gardner, 1928, *Chione chipolana* Dall, 1903, *Linga glenni* (Dall, 1903), *Armimiltha chipolana* (Dall, 1903), and *Pteria chipolana* Dall, 1898.

Species of *Rhyncholampas* inhabit environments similar to other cassiduloids, preferring sandy substrates in which they are infaunal to semi-infaunal dwellers, and water depths of intertidal zones to greater than 20 meters (Kier, 1962; 1975). *Rhyncholampas chipolanus*, n. sp., was collected from sandy sediments and appears to fit the generalized ecologic conditions typical for cassiduloids.

Additional collecting at UF locality CA025 and a search of the collections of Chipola Formation materials at Tulane University, the Hoerle Collection at the National Museum of Natural History, the Florida Museum of Natural History (FLMNH), and the Florida Geological Survey Collection (recently transferred to the FLMNH) yielded no additional specimens.

Other echinoids previously found in the Chipola Formation include *Echinocyamus chipolanus* Cooke, 1942, and an undescribed brissid. The Chipola Formation echinoderm fauna, as well as the rest of the Florida Miocene echinoderm fauna is inadequately documented, due mainly to poor preservation and collector bias (Oyen and Portell, 1993; 1994). Currently, Portell and Oyen are conducting additional studies that should yield a number of new Florida Miocene taxa.

ACKNOWLEDGMENTS

Andrew and Greta Murray of Bradenton, Florida are thanked for discovering the holotype and for donating this rare specimen, along with many other rare taxa, to the Florida Museum of Natural History. Emily and Harold Vokes permitted access to the Tulane University Collection. Thomas Waller and Warren Blow provided assistance while examining the Hoerle Collection of Chipola Formation fossils at the National Museum of Natural History. Burchard Carter, Georgia Southwestern College and Stephen Donovan, University of the West Indies kindly reviewed the manuscript. This is University of Florida Contribution to Paleontology 471.

SYSTEMATIC PALEONTOLOGY

Class ECHINOIDEA Leske, 1778
Order CASSIDULOIDA Claus, 1880
Family CASSIDULIDAE
A. Agassiz and Desor, 1847
Genus RHYNCHOLAMPAS
A. Agassiz, 1869

PLATE 1

Figures

1a-1b. *Rhyncholampas chipolanus* Oyen and Portell, n. sp.; UF 66633 (holotype).
1a. Adapical view, x1.
1b. Adoral view, x1.

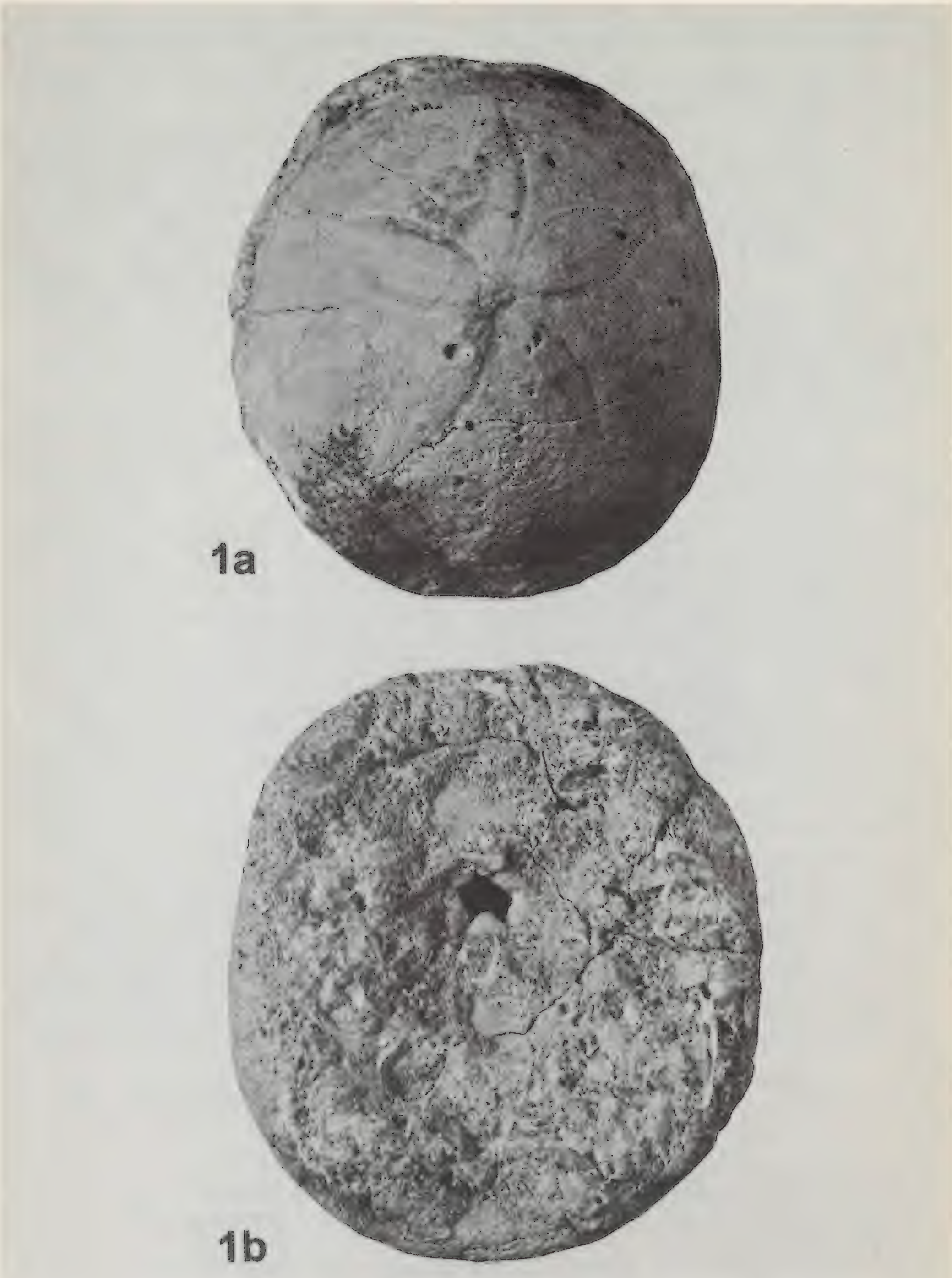

PLATE 1

Rhyncholampas A. AGASSIZ, 1869, Bull. Mus. Comp. Zool., v. 1, p. 270.

Type species: *Pygorhynchus pacificus* A. Agassiz, 1863, by subsequent designation, Lambert, 1918.

RHYNCHOLAMPAS CHIPOLANUS
Oyen and Portell, n. sp.
Plate 1, figures 1a,b
Plate 2, figures 2a,b

Description:

Diagnosis: Species characterized by slightly truncated oval outline, moderately sloping sides with focused peak at apical system, depressed adoral surface, nearly closed lanceolate petaloid ambulacra, and pentagonal periproct.

Shape: Large, having test length of 77.8 mm; width relatively uniform and measures 64.9 mm at mid-length of test; margin relatively sharp and angular in posterior, subrounded to moderately truncated along lateral margins; height measures 40.3 mm from adoral surface to peak at apical system; highest point at apical system, slightly anterior of test center; sides slope moderately with slightly shallower slope in upper half and slightly steeper slope in lower half of specimen.

Apical System: Located central to slightly anterior of test length midpoint; compact size.

Ambulacra: Petals well developed, broad, lanceolate, with greatest width at approximately 35% of petal length; petals I and V are longest, III is slightly shorter, and II and IV are shortest; petals extend about 65% of distance to test margin; petal widths nearly equal, with petal III 25% narrower than others; petals almost closed at distal end.

Periproct: Supramarginal; width approximately 1.5x greater than height; pentagonal shape with apex oriented toward apical system; slight groove extending from opening to posterior margin; base of opening located 10.4 mm above adoral surface.

Peristome: Moderately anterior, pentagonal, and depressed; width approximately 1.7x greater than anterior-posterior length; anterior margin of opening located 26.9 mm from anterior test margin.

Floscelle: Bourrelets distinct and pointed.

Tuberculation: Adapical tubercules small and uniformly distributed; limited visible adoral tubercules near peristome are distinctly larger.

Holotype: UF 66633; length 77.8 mm, width 64.9 mm, and height 40.3 mm.

Type locality: UF locality CA025, west bank of the Chipola River, approximately 0.5 miles upstream from the mouth of Fourmile Creek, Calhoun County, Florida (NW1/4, SW1/4, Sec.29, T1N, R9W, Clarksville Quadrangle USGS 7.5' series).

Occurrence: Chipola Formation, northwestern Florida; early Miocene.

Etymology: Named for the Chipola River from whose bank the holotype was collected.

Discussion: Rhyncholampas chipolanus, n. sp., is extremely rare, with only one specimen known and available for examination. Comparison with the Pliocene species *Rhyncholampas ayresi* Kier, 1963, from the Caloosahatchee Formation in Florida shows only minor morphological similarities. *Rhyncholampas chipolanus* is distinguished from *R. ayresi* by its angular adapical-adoral surface contact, lower width-to-length and height-to-length ratios, pentagonal periproct, concave adoral surface, and its more conical adapical shape. Comparison with another Pliocene species, *Rhyncholampas evergladensis* (Mansfield, 1932), shows a stronger morphological resemblance. Both *R. chipolanus* and *R. evergladensis* have similar width-to-length ratios (of approximately 0.83), a concave adoral surface, a transverse oriented periproct, and the test length of *R. chipolanus* falls within the

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PLATE 2

Figures

2a-2b. *Rhyncholampas chipolanus* Oyen and Portell, n. sp.; UF 66633 (holotype).
2a. Posterior view, x1. Note pentagonal shape of periproct with apex of pentagon directed upward.
2b. Lateral view showing general conical shape of test with the peak of the cone located approximately at apical system, x1.

3. *Rhyncholampas evergladensis* (Mansfield, 1932); UF 24524, x1. Lateral view showing less conical shape of test in comparison with the new species shown in Figure 2b.

2a

2b

3

PLATE 2

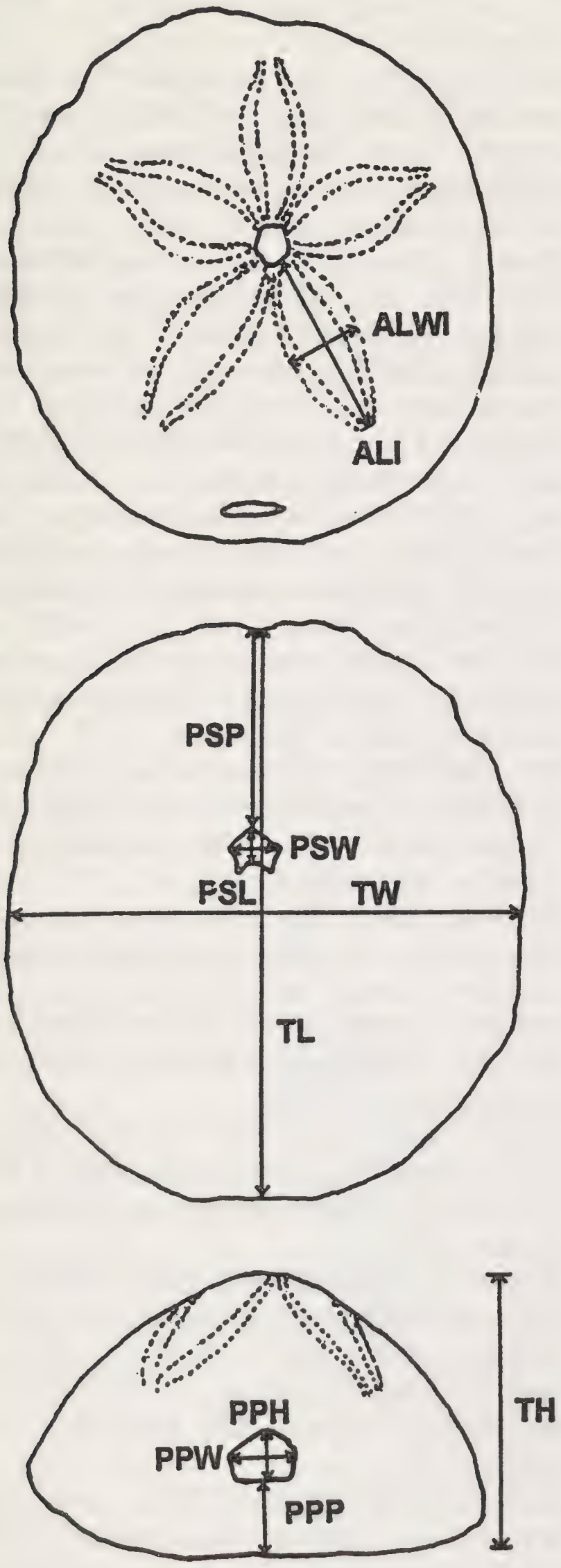
size range for test lengths of *R. evergladensis* as described by Kier (1963).

However, differentiation of the two species can be accomplished using several characteristics. *Rhyncholampas chipolanus* has adapical ambulacral petals that terminate slightly more proximally to the apex and are nearly closed but petals on *R. evergladensis* remain distinctly open and extend further toward the test margin. The distal petaloid ambulacral width (when expressed as the ratio of distal petal width to test length) averages 0.040 for *R. chipolanus,* while the ratio averages 0.073 for the sample population of ten individuals of *R. evergladensis.* Since only a single holotype specimen exists, no statistical tests for significance can be used to compare the mean ratios of petaloid distal width between the two species. It does, however, support the visual estimate and interpretation that the petal widths (at the distal ends near the test margin) are different. The periproct is transversely oriented in both species, but in *R. chipolanus* it is pentagonal in outline, with the apex of the pentagon pointing up (*i.e.,* adapical), whereas the periproct of *R. evergladensis* is more oval or elliptical shaped, and the lower edge of the opening is depressed slightly downward (toward the adoral surface). Finally, *Rhyncholampas chipolanus* has a more highly peaked, conical, apical system but most of the 50 specimens of *R. evergladensis* examined in the Florida Museum of Natural History have a less conical adapical surface (see Plate 2, figures 2 and 3). It should be noted that several specimens do have surfaces approaching a conical shape, but none to the degree found in the newly described species. Furthermore, the very few specimens of *R. evergladensis,* which are more conical in form, represent an exceptionally small percentage of the total sample population examined during the course of this comparison.

Comparison with other species of *Rhyncholampas* known from the Tertiary resulted in no other close morphological matches. *Rhyncholampas gouldii* (Bouve, 1846), an Oligocene cassiduloid from the Suwannee Limestone, has modest shape similarities, but none of the hundreds of specimens examined or measured in the FLMNH collections have test lengths within approximately 20 mm of *R. chipolanus,* and the width-to-length ratio of *R. gouldii* is significantly greater than in *R. chipolanus* (W/L ratio averages approximately 0.92; Oyen, unpubl. data). Five species and subspecies of *Rhyncholampas* are known from the Eocene in Florida, but none of these taxa have morphologic resemblance to *R. chipolanus.* All are significantly smaller and have distinctly different test shapes and, therefore, have no effect on this taxonomic description and species designation. Both of the valid Cuban species, *R. rodriguezi* and *R. cervatesi* Sanchez Roig, 1949, (an Oligocene species) are much too small to be considered reasonable for comparison with *R. chipolanus.* Overall body size as interpreted from test length measurements seems to limit the reasonable species comparisons to the two Pliocene species of *R. ayresi* and *R. evergladensis.* A thorough review of taxonomic synonymies described in Kier (1962, 1963) and Kier and Lawson (1978) revealed no other potential species that are morphologically similar or of appropriate age to dissuade this species designation.

Another aspect of support for our interpretation is the length of species durations exhibited in other echinoids from the Cenozoic. Based on stratigraphic distributions in Florida, it is rare for echinoid species to be found in more than one stratigraphic unit (although this fact is a function of the current stratigraphic status of the various formations). In any case, the temporal range for known echinoid species from the southeastern U.S. is relatively short. One would expect to have a unique species of *Rhyncholampas* present in the Miocene since the prior species known is *R. gouldii* from the Oligocene and the subsequent species known is *R. evergladensis* from the Pliocene. Using Sr isotopic age calculations, Jones *et al.* (1993) determined the age assigned to the Suwannee Limestone (early Oligocene) to be approximately 34.8 Ma, and the age assigned to the Chipola Formation (early Miocene) to be approximately 18.7 Ma. The age assigned to the Tamiami Formation (early Pliocene) cannot be resolved to a single age value using Sr isotopic calculations alone because of limitations in the technique, but Jones *et al.*

(1991) have estimated the potential age range for a portion of the Tamiami Formation exposed near Sarasota, FL to be constrained within an age range older than 3.0 Ma (using Sr isotopic age calculations) and restricted to the early Pliocene. Using Harland *et al.* (1989), the age applied to the early Pliocene starting time



BIOMETRIC MEASUREMENTS

<u>Test Dimensions</u>	
Test Length (TL)	= 77.8 mm
Test Width (TW)	= 64.9 mm
Test Height (TH)	= 40.3 mm
<u>Peristome Dimensions</u>	
Peristome Length (PSL)	= 4.3 mm
Peristome Width (PSW)	= 7.2 mm
Peristome Position (PSP)	= 26.9 mm
<u>Periproct Dimensions</u>	
Periproct Width (PPW)	= 10.3 mm
Periproct Height (PPH)	= 6.8 mm
Periproct Position (PPP)	= 10.4 mm
<u>Ambulacra Dimensions</u>	
Amb. I Length (ALI)	= 32.1 mm
Amb. II Length (ALII)	= 25.8 mm
Amb. III Length (ALIII)	= 29.8 mm
Amb. IV Length (ALIV)	= 26.9 mm
Amb. V Length (ALV)	= 32.8 mm
Amb. I Width (ALWI)	= 10.8 mm
Amb. II Width (ALWII)	= 11.6 mm
Amb. III Width (ALWIII)	= 8.5 mm
Amb. IV Width (ALWIV)	= 11.4 mm
Amb. V Width (ALWV)	= 10.8 mm

TEXT-FIGURE 1

This figure illustrates the location where biometric data from morphological features were derived. Morphologic trait abbreviations are associated with full name in biometric data table provided next to the specimen illustrations.

is 5.2 Ma, therefore the early Pliocene (which includes the *R. evergladensis* - bearing Tamiami Formation) is likely found within an age range of about 3.0 to 5.2 Ma. Thus, the species distribution gap for *Rhyncholampas* was from 34.8 to 5.2 Ma, which is an exceptionally large interval of time to have no species evolve within the genus, and the addition of another species (*R. chipolanus*) to the record of this genus is reasonable and would be an expected component to fill the temporal and stratigraphic gap of species distribution in this Cenozoic echinoid genus.

Several important points regarding the measurements should be noted, and the biometric measurements taken on the holotype specimen are provided in Textfigure 1 as well as illustrations showing measurement positions. The test width (TW) was measured at the midpoint of the test length (TL). Test height (TH) is the maximum height from the adoral surface to the peak at the apical system. Periproct height (PPH) was measured at the midpoint of the periproct width (PPW), and the peristome width (PSW) is the maximum width. Finally, all ambulacrum lengths (ALI - ALV) were measured from the apical system margin to the last pore pair of each petal and ambulacrum widths (ALWI - ALWV) were measured at the maximum width between outer pores on the petal.

LOCALITY DATA

The following is a collecting locality of the Invertebrate Paleontology Division, Florida Museum of Natural History, University of Florida (UF) in the early Miocene, Chipola Formation.

CA025 West bank of the Chipola River, approximately 0.5 miles upstream from the mouth of Fourmile Creek, Calhoun County, Florida (NW1/4, SW1/4, Sec.29, T1N, R9W, Clarksville Quadrangle USGS 7.5' series). Equivalent to Tulane University locality 1545.

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July 31, 1996

A NEW SPECIES OF *POIRIERIA (PAZIELLA)* (GASTROPODA:MURICIDAE) FROM THE PUNTA GAVILAN FORMATION, NORTHERN VENEZUELA

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When Rutsch originally described the molluscan fauna of the Pliocene Punta Gavilan Formation, northern Venezuela (1934), he included only two muricid species. These are: *Murex recurvirostris* Broderip, 1833 [later assigned to the Recent *Haustellum donmoorei* (Bullis, 1964) by Vokes, 1990, p. 18], and *Murex domingensis* Sowerby, 1850 [= *Chicoreus (Siratus) domingensis* in Vokes, 1990, p. 50]. Subsequently, the living species *Chicoreus (Chicoreus) brevifrons* (Lamarck, 1822) was added to the fauna (Vokes, 1990, p. 35). Later (Vokes, 1992, p. 41), the Gatun species *Poirieria (Panamurex) gatunensis* (Brown and Pilsbry, 1911) was also added and, at the same time, *Poirieria (Panamurex) rutschi* was described (Vokes, 1992, p. 52, pl. 11, figs. 1-4) from the fauna. Most recently, a Punta Gavilan specimen of the living *Murexiella (Murexiella) macgintyi* (Smith, 1938) was figured (Vokes, 1994, p. 104, pl. 14, fig. 3).

Thus, the muricid fauna has grown to six in number and, of these, three are species found living today in the waters off Venezuela. Of the other three, *P. rutschi* is closely related to the Recent *Poirieria (Panamurex) velero* Vokes, 1970, and *C.(S.) domingensis* is thought to be ancestral to the living *C.(S.) springeri* (Bullis, 1964). Only *P. gatunensis* evidently has no living counterpart in the local fauna.

Two of these Recent analogs of the Punta Gavilan fauna were described in a landmark paper on the hitherto almost unknown deep-water fauna from off northeastern South America by Harvey Bullis (1964). In that same paper a third spectacular species of *Paziella* was named *Murex (Poirieria) oregonia* (Bullis, 1964, p. 106, figs. 5, 6), with the type material coming from 105 to 275 fathoms [192-503 meters], at locations ranging from Trinidad to the Amazon River.

Therefore, it was not totally unexpected to see a specimen recently collected at Punta Gavilan by Bernard Landau of what, at first glance, appreared to be *P. oregonia*. However, closer examination shows the incomplete specimen to have a combination of traits of *P. oregonia* and the smaller *Poirieria (Paziella) nuttingi* (Dall, 1896), which so far as we know is limited to the Gulf of Mexico. Although the holotype of *P. nuttingi* came from only 27 meters, off Key West, Florida, most examples come from depths of approximately 200 meters.

Although the Punta Gavilan specimen is an incomplete, silicified replacement, all of the essential characteristics of the species are preserved and, given the unlikely possibility of collecting a better example, I have concluded that the presence of this unusual species warrants description.

POIRIERIA (PAZIELLA) LANDAUI

Vokes, n. sp.

Text-figure 3

Description: Shell large for the subgenus; six teleoconch whorls in holotype, probably eight in completely adult shell; protoconch unknown. Spiral ornamentation on spire whorls of two simple cords, with a slightly stronger cord at shoulder. On body whorl, five cords anterior to shoulder, plus one additional cord on siphonal canal. Axial ornamentation presumed to be of eight thin, only slightly raised, lamellar varices on each whorl, undulated by spiral cords; only at intersection of varices with cords at shoulder and siphonal canal short, open spines produced. Suture deeply impressed, subsutural ramp almost perpendicular to shell axis. Aperture poorly preserved but presumably with a smooth appressed columellar lip and a denticulate outer lip. Siphonal canal short, broad, distally recurved, giving rise to a marked siphonal fasciole.

Holotype: Naturhistorisches Museum Basel NMB H-17775; height 58.8 mm, diameter (as is) 32.2 mm.

Type locality: Punta Gavilan Formation; Punta Gavilan, Edo. de Falcon, Venezuela.

Occurrence: Known only from the type locality.

Etymology: Named in honor of Bernard M. Landau, of Albufeira, Portugal, who collected the holotype specimen.

Discussion: The traits that *P.(P.) landaui* shares with *P.(P.) oregonia* includes the large size and the relatively strong (compared to *P. nuttingi*) spiral cords. However, in most aspects the new species has more in common with *P. nuttingi*, including the broader shell outline, with a

shorter broader siphonal canal and marked siphonal fasciole. The number of spiral cords anterior to the shoulder in most specimens of *P. nuttingi* is about four (the holotype is rather "atypical" with two additional secondary spirals),-in *P. landaui* it is five, and in *P. oregonia* it is six. Both *P. nuttingi* and *P. landaui* have a single row of spines on siphonal canal, in contrast to the two rows in *P. oregonia*.

As noted by Bullis (1964, p. 106), *P. oregonia* is more than twice as large as *P. nuttingi* with the same number of whorls; both holotypes (text-figure 1, *P. nuttingi*; text-figure 2, *P. oregonia*) have eight whorls. A specimen of *P. landaui* with eight whorls would approximate the size of *P. oregonia*. The shell outline in *P. landaui* is lower-spired than either of the other two species.

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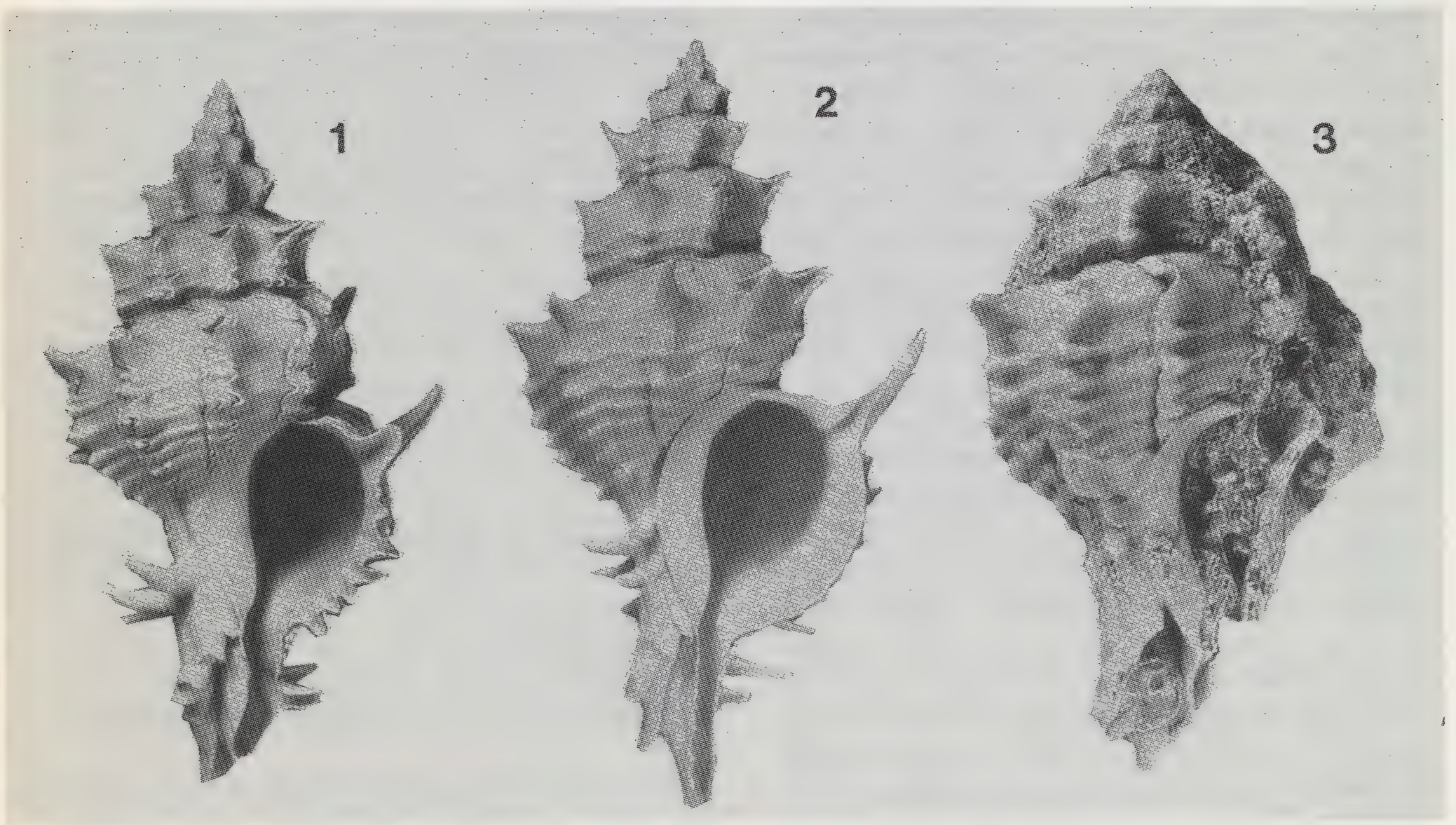

Text-figure 1, *Poirieria (Paziella) nuttingi* (Dall); USNM 107372 (holotype); height 44.4 mm, diameter 20.5 mm (excluding spines) (X 1 1/2). Text-figure 2, *Poirieria (Paziella) oregonia* (Bullis); USNM 635149 (holotype); height 85.2 mm, diameter 37.8 mm (excluding spines) (X 3/4). Text-figure 3, *Poirieria (Paziella) landaui,* n. sp.; NMB H-17775 (holotype); height 58.8 mm, diameter 32.2 mm (as is) (X 1).

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CENOZOIC MURICIDAE OF THE WESTERN ATLANTIC REGION. PART XII – THE SUBFAMILY OCENEBRINAE (IN PART)

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I. ABSTRACT

Sixteen species assigned to the muricid subfamily Ocenebrinae are treated, comprising only those species characterized by having (in all but possibly one case) a sealed siphonal canal. Nine genus-groups are included, of which three, all from the Haywood Landing Member of the Belgrade Formation (latest Oligocene, North Carolina), are new. These are: *Fenolignum* (type: *F. umbilicatum*, n. sp.), *Argyrobessa* (type: *Murex kellumi* Richards, 1943), and *Pteropurpura (Odontopurpura)*, n. subgen. (type: *Tritonalia festivoidea* Vokes, 1963). There are few taxa in any of the genus-groups; six are monotypic, including the three new taxa, and the previously described genera *Miocenebra, Ocinebrina,* and *Ceratostoma*. The remaining genus-groups have only a small number of species included: *Pteropurpura* s.s. (3); *Pterorytis* s.s. (3), and *Pterorytis (Microrhytis)* (4). Of the 16 species treated, four are new: *Ocinebrina francesae* and *Pterorytis (Microrhytis) christopheri*, from the Early Miocene Cantaure Formation, Venezuela; *Pteropurpura (Pteropurpura) boesei*, from the Santa Rosa beds, Veracruz, Mexico; and *Fenolignum umbilicatum*, from the Haywood Landing Member, Belgrade Formation, North Carolina. The genera treated are largely extinct, at least in the western Atlantic, although *Ocinebrina* and *Ceratostoma* survive elsewhere, and only one of the included species, *Pteropurpura bequaerti*, still lives in the waters of the western Atlantic.

II. INTRODUCTION

The Muricidae is a large family of neogastropods comprising at least eight subfamilies, all united by the presence of an accessory boring organ in the foot. Some of the component subfamilies, such as the Trophoninae, have received little study and are recognized mainly on the basis of primitive characters; but others, such as the Muricinae, Ocenebrinae, and Rapaninae, have been the subjects of intense anatomical investigation, and are reasonably well-defined clades.

In this paper we treat the subfamily Ocenebrinae in part. After surveying the group's characters, we have limited this work to include only the fossil and living western Atlantic ocenebrines with a sealed siphonal canal, although one of the taxa (*Argyrobessa*, new genus) possibly may have had an open canal. A complete list of taxa now included in the subfamily

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Ocenebrinae may be found in the Appendix at the end of this work.

III. ACKNOWLEDGMENTS

The writers are profoundly grateful to a number of persons and institutions for the loan of material, as well as valuable information on distribution of species. The institutions include the Academy of Natural Sciences, Philadelphia (Gary Rosenberg, Elana Benamy), the United States Museum of Natural History (Thomas R. Waller, Warren C. Blow), and the Naturhistorisches Museum, Basel, Switzerland (Peter Jung). Among individuals our greatest debt is to Susan B. Stephens, Sanibel, Florida, who generously provided much of the material figured herein. Others include Lyle Campbell, Spartanburg, South Carolina; Mr. and Mrs. William J. Fulton, Chamblee, Georgia; the late Robert V. Blow, Portsmouth, Virginia; Andrew and Greta Murray, Bradenton, Florida; Mr. and Mrs. Jack Gibson Smith, Surrey, England; Lauck W. Ward, Virginia Museum of Natural History, Martinsville, Virginia; William K. Emerson, American Museum of Natural History (Emeritus); and Joseph G. Carter, University of North Carolina, Chapel Hill, North Carolina. GJV acknowledges partial funding of this research by NSF Grant EAR-94-05537.

ABBREVIATIONS FOR REPOSITORY INSTITUTIONS

MCZ – Museum of Comparative Zoology, Harvard University, Cambridge, MA
NMB – Naturhistorisches Museum, Basel, Switzerland
PRI – Paleontological Research Institution, Ithaca, NY
TU – Tulane University, New Orleans, LA
UCMP – University of California, Museum of Paleontology, Berkeley, CA
UF – Florida Museum of Natural History, Gainesville, FL
USNM – United States National Museum of Natural History, Washington, DC

IV. SYSTEMATIC PALEONTOLOGY

Family MURICIDAE Rafinesque, 1815
Subfamily OCENEBRINAE Cossmann, 1903

Discussion: Cossmann (1903) was the first author to divide the Muricidae into subfamilies. He proposed the Ocenebrinae for muricids with a purpuroid operculum and a varicate shell. The Rapaninae also have a purpuroid operculum, but their shells lack varices. Distinction on the basis of these characters, however, is inadequate. There are many Ocenebrinae without varices, and some varix-bearing muricids with a purpuroid operculum appear to belong to subfamilies other than Ocenebrinae. Many members of the Ergalataxinae, for example, have a purpuroid operculum as well as a shell characterized by one or more varices (see Houart, 1995).

In her subfamilial revision, Vokes (1964) concluded that the operculum provided no diagnostic characters to distinguish the Muricinae from the "Tritonaliinae" (= Ocenebrinae). According to Vokes, the only conchological feature useful for separating muricids at the subfamilial level is the sealed siphonal canal, which is found only in the Ocenebrinae and Typhinae. The latter subfamily differs dramatically from the Ocenebrinae in shell characters such as the presence of tubular shoulder spines, and the two groups are probably not closely related. Other muricid subfamilies, as well as many Ocenebrinae, have an open siphonal canal.

Vokes (1964) argued that the radula provides the best characters for separating muricid subfamilies. Members of the Ocenebrinae have a central rachidian tooth on which there are three larger teeth in the central part, flanked by numerous smaller teeth on the margins. Vokes (1971) transferred *Homalocantha* (with a purpuroid operculum and open siphonal canal) and *Purpurellus* (with a muricine radula and operculum and a sealed canal) to the subfamily Muricinae. She also removed from the Ocenebrinae the genera *Eupleura, Urosalpinx,* and *Crassilabrum.* In 1971, therefore, it was Vokes' view that the Ocenebrinae comprised the genera *Ocenebra* (formerly *Tritonalia*), including the subgenera *Hadriania, Miocenebra,* and *Ocinebrina; Jaton,* with subgenera *Pterorytis* and *Ceratostoma;* and *Pteropurpura,* with subgenera *Ocinebrellus, Calcitrapessa,* and *Poropteron.* All

these genera have a sealed siphonal canal. Vokes (1971, p. 7) noted that "*Eupleura,* together with *Vitularia, Crassilabrum, Hanetia,* and *Urosalpinx,* belong in yet another subfamily characterized by having an open siphonal canal, a purpuroid operculum, and a radula similar to that of the Ocenebrinae."

Following Kool (1993) and Vermeij and Kool (1994), we now include as members of the Ocenebrinae not only the above mentioned genera with a sealed siphonal canal, but also *Eupleura, Crassilabrum,* and *Urosalpinx*, as well as a probable clade of "*Thais*-like" genera in which the non-varicate collabral sculpture is reduced or wholly absent. These genera include *Acanthina, Acanthinucella, Chorus, Ecphora, Haustrum, Lepsiella, Nucella, Spinucella, Trochia,* and *Zulloia,* and a genus of Neogene labral-tooth-bearing species being described by T.J. DeVries and G.J. Vermeij. Other ocenebrine genera with an open siphonal canal and well-developed collabral sculpture include *Forreria, Pterynopsis, Namamurex,* and *Vokesinotus.*

Using shell characters, we define the Ocenebrinae as follows: muricids with crenulated, planar outer lip; inner side of outer lip smooth or with denticles, usually deeply recessed; lirae on inner side of outer lip absent; anal notch absent (except in *Hadriania* and *Miocenebra*); inner lip smooth; posterior end of aperture broadly rounded, not angulated or adapically pointed; apical end of outer lip not adapically extended; parietal rib and columellar folds absent.

Ocenebrines differ from many members of the Muricinae by lacking a parietal rib at the apical end of the inner lip. Those muricines lacking a parietal rib differ from Ocenebrinae by having lirae on the inner side of the outer lip. A few ocenebrines, including *Roperia* and individuals of *Acanthinucella spirata* (Blainville, 1832), *A. punctulata* (Sowerby, 1835), and *Nucella emarginata* (Deshayes, 1839), possess a parietal knob. They differ from members of the Muricinae by the absence of varices, by having a dentate rather than lirate outer lip, and by lacking the adapical extension of the outer lip.

The subfamily Ocenebrinae differs from Rapaninae by the absence of a subsutural cord, the absence of a parietal rib, and by having a rounded rather than angulate or pointed apical end of the aperture. Rapanines tend to have the apical end of the outer lip adapically slightly extended, often forming a gutter-like extension of the aperture by virtue of the presence of the parietal rib on the apical end of the inner lip (see Vermeij and Kool, 1994). Many members of the Rapaninae possess an anal notch or sinus, one or more folds on the columella, and lirae on the inner side of the outer lip, all features lacking in Ocenebrinae.

Some members of the Ergalataxinae resemble many Ocenebrinae in possessing varices. They differ from ocenebrines by having a lirate outer lip, a parietal rib, and usually one or more folds on the anterior part of the columella.

Although a sealed anterior siphonal canal occurs in several unrelated muricid groups, it is especially characteristic of a number of genera in the Ocenebrinae, including *Ocenebra, Ceratostoma, Pteropurpura, Fenolignum* (new genus), *Ocinebrina, Jaton, Hadriania, Miocenebra, Pterorytis,* and several undescribed taxa. All are characterized by strong axial sculpture, which in many cases includes varices. Here we treat western Atlantic representatives of these taxa.

The groups treated in this paper are unusual in having left few living descendants. Of the sixteen species we deal with in this paper, only one is still living in the western Atlantic. The muricid fauna of the Haywood Landing Member of the Belgrade Formation (latest Oligocene) of North Carolina is especially remarkable for the large number of unusual genera and species. In this paper, we treat no less than four monotypic genera, three of which are newly proposed, and none of which is known beyond Early Miocene time.

Genus OCENEBRA Gray, 1847

Tritonalia FLEMING, 1828, History British Animals, p. 564 (index) and corrigenda (? *n.n. pro Triton* Montfort, 1810, *non* Linnaeus, 1758).

Type species: *Murex erinaceus* Linnaeus,

1758, by subsequent designation, Gray, 1847.

Ocenebra "Leach MS" GRAY, 1847, Ann. Mag. Nat. Hist., v. 20, p. 269 (?October); GRAY, 1847, Zool. Soc. London, Proc., pt. 15, p. 133 (November).

Type species: *Murex erinaceus* Linnaeus, 1758, by monotypy (?Oct.) or original designation (Nov.).

Inermicosta JOUSSEAUME, 1880, Le Naturaliste, Année 2, no. 42, p. 335.

Type species: *Murex fasciatus* "Sowerby, 1841" (not *M. fasciatus* Gmelin, 1791 = *Tritonalia inermicosta* Vokes, 1964), by original designation.

Discussion: The names *Ocenebra* and Ocenebrinae have replaced the questionably proposed *Tritonalia* Fleming, 1828, and Tritonaliinae by a ruling of the International Commission on Zoological Nomenclature, Opinion 886, 1969. The use of "*Ocinebra*" represents an incorrect spelling of *Ocenebra*.

In the past, *Ocenebra* has been used as a grab-bag for a wide variety of fossil and living ocenebrines*. We here restrict the taxon *Ocenebra* to a relatively small number of Miocene to Recent species from western Europe, the Mediterranean region, and tropical West Africa. These are characterized by the tendency to form three varices on the last whorl, by the presence of six to eight primary spiral cords on the last whorl, a crenulated outer lip without a labral tooth, an adherent or very lightly erect inner lip, and six weak to strong denticles on the inner side of the outer lip. In species with varices, the latter are separated from each other by a single intervarical node. There appears to be considerable variation in expression of axial sculpture in the type species, *O. erinaceus*. Many individuals lack varices on the last whorl and instead are characterized by sharp-edged axial ribs that are not differentiated into varices and intervarical nodes.

Two fossil western Atlantic species discussed below may be related to *Ocenebra*, but they differ in several significant ways from the type species, *O. erinaceus* (Linnaeus), and other closely related members of *Ocenebra*. One of these fossil species, originally described by Vokes (1963) as *Tritonalia (Miocenebra) silverdalense,* is treated here as belonging to the distinct genus *Miocenebra* Vokes, 1963. For the other, we propose the new genus *Fenolignum*. Inter-relationships among taxa of the Ocenebrinae cannot be resolved until all the genera are considered in a phylogenetic context. Rather than considering *Miocenebra* and *Fenolignum* as subgenera of *Ocenebra,* we have elected to treat them as full genera pending the outcome of phylogenetic analysis.

*For example, Abbott (1974, p. 184) referred to the genus *Ocenebra* several western Atlantic species that we believe are better placed in the Muricopsinae (see Vokes, 1994). These are: *muricoides, schrammi,* and *rosea* [now referred to *Muricopsis (Risomurex)*]; *minirosea* and *micromeris* [now *Favartia*]; and *emipowlusi* [now *Murexsul*].

Genus FENOLIGNUM, n. gen.

Type species: *Fenolignum umbilicatum,* new

PLATE 1

Figures Page

1-5. *Fenolignum umbilicatum*, n. sp 74

1. (X 2) USNM 488706 (holotype); height 24.1 mm, diameter 15.2 mm.
   Locality: TU 866; Haywood Landing Member, Belgrade Formation.
2. (X 2) USNM 488707 (paratype A); height 24.6 mm, diameter 16.0 mm.
3. (X 6; X 10) USNM 488708 (paratype B); height 7.5 mm, diameter 5.0 mm.
4. (X 2) Fulton Collection (paratype C); height 19.0 mm, diameter 13.3 mm.
5. (X 3) USNM 488709 (paratype D); height 16.0 mm (incomplete); diameter 10.6 mm (incomplete).
   Locality of all: same as holotype.

6. *Miocenebra silverdalensis* (Vokes) 75

(X 2) USNM 644380 (holotype); height 28.5 mm, diameter 12.4 mm.
Locality: TU 562; Haywood Landing Member, Belgrade Formation.

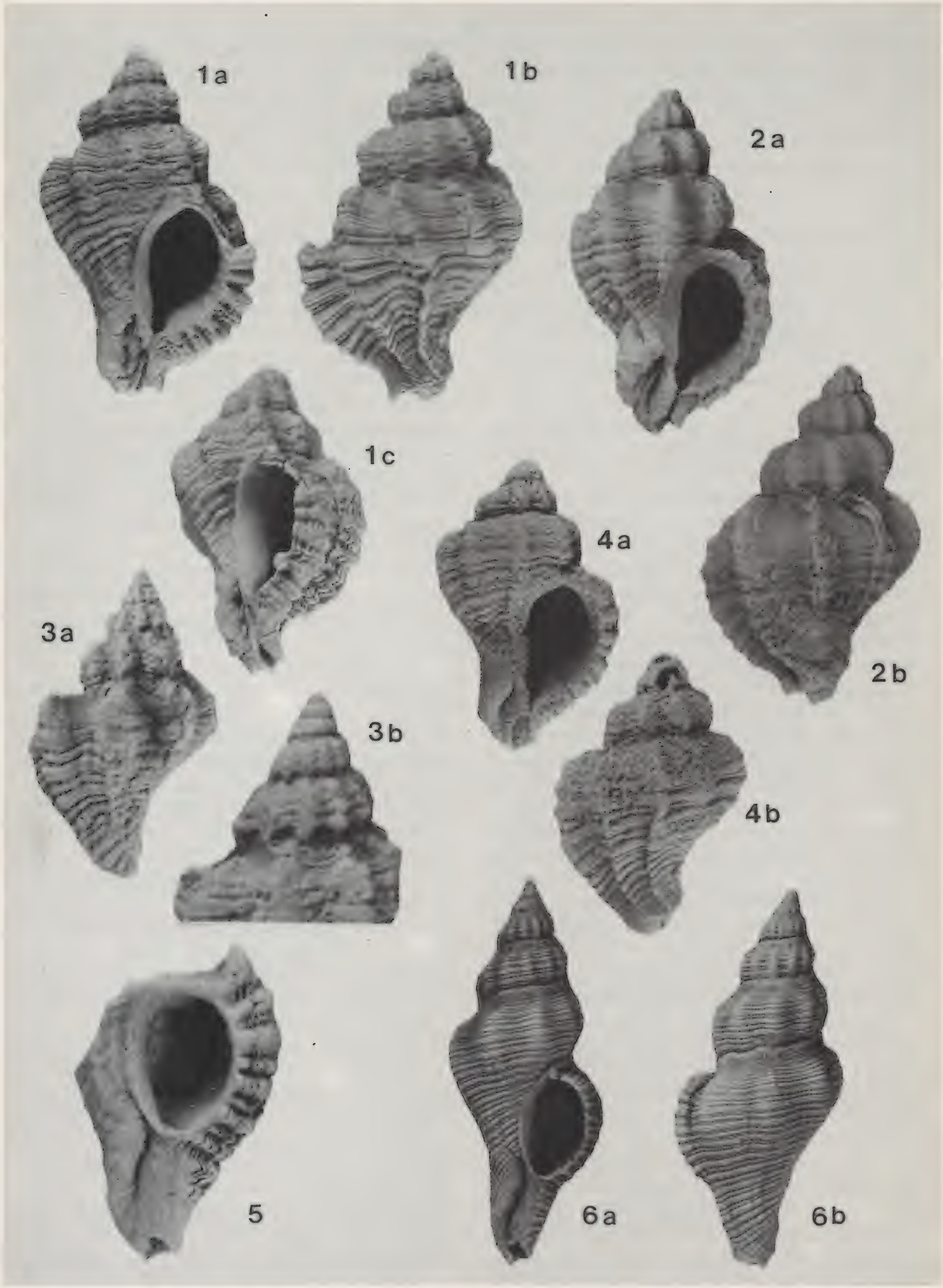

PLATE 1

species.

Description: Fusiform ocenebrine shell with external sculpture consisting of eight strong axial ribs crossed by about nine spiral cords on the body whorl; one of the spiral cords near the base terminating on the outer lip in a small, blunt labral tooth; anterior siphonal canal short, sealed; inner side of outer lip with about eight weak elongate denticles; outer lip erect in adults; inner lip adherent along its entire length; umbilical slit present.

Etymology: fenum (Latin: hay) and *lignum* (Latin: wood), for the Haywood Landing Member of the Belgrade Formation, type stratum for the type species.

Discussion: Among the many unusual muricids in the Late Oligocene beds near Silverdale, North Carolina, is a small broadly fusiform species whose combination of characters places it outside the limits of any ocenebrine genus recognized thus far. It differs from *Ocenebra* by the presence of a labral tooth formed at the termination of a basal cord, and by the absence of differentiated varices and intervarical nodes, instead having axial ribs that extend from a low shoulder to the base. *Fenolignum* is similar to some European species such as *"Ocenebra" curvicosta* (Grateloup, 1847) and *"O." striaeformis* (Michelotti, 1841) from the Early Miocene of France and Italy in having a labral tooth at the end of a spiral cord, but the European taxa differ strongly from *Fenolignum* by having a thickened outer lip and by having abaperturally reflected axial ribs terminating on the labral tooth-bearing cord. *Fenolignum* also bears a superficial resemblance to *"Ocenebra" lugubris* (Broderip, 1833) living in the Panamic Province, but the latter species possesses strongly recurved varices and a labral tooth arising from a groove rather than from a cord. Moreover, the Panamic species lacks dentition on the inner side of the outer lip.

Fenolignum umbilicatum, n. sp.
Plate 1, figures 1-5

Description: Shell with six teleoconch whorls; protoconch of two and one-half small, conical whorls; teleoconch ornamentation beginning gradually, there being no line of demarcation between protoconch and teleoconch. Axial sculpture on first teleoconch whorl consisting of twelve rounded ridges, becoming increasingly inflated with each successive whorl; on body whorl eight axial ribs. On about fourth teleoconch whorl, small open flanges appearing on abapertural side of ridges, consisting of multiple laminae, best developed on siphonal canal. Spiral ornamentation consisting of heavy spiral cords, approximately nine on body whorl and two additonal ones on canal. Numerous fine spiral threads covering entire shell surface, including primary spiral cords. Adapertural faces of axial ribs fimbriated elaborately in harmony with primary and secondary spiral ornamentation. Suture deeply impressed, giving whorls a rounded contour with a low shoulder. Aperture oval; inner lip narrow, adherent along entire length, smooth; margin of outer lip crenulated by spiral cords; about eight weak, elongate denticles on inner side of outer lip. Fifth primary cord counting from suture ending in blunt labral tooth on edge of outer lip above base of canal. Siphonal canal short, broad, sealed by an extension from the columellar lip to apertural side. Small umbilical slit below continuous fasciole.

Holotype: USNM 488706; height 24.1 mm, diameter 15.2 mm.

Type locality: TU 866, Haywood Landing Member, Belgrade Formation (= "Silverdale beds"); marl pit on north side of Webb Creek and east side of unnumbered county highway, Silverdale, Onslow County, North Carolina.

Paratype A: USNM 488707; height 24.6 mm, diameter 16.0 mm.

Paratype B: USNM 488708; height 7.5 mm, diameter 5.0 mm.

Paratype C: Fulton Collection; height 19.0 mm, diameter 13.3 mm.

Paratype D: USNM 488709; height 16.0 mm (incomplete), diameter 10.6 mm (incomplete).

Locality of all, same as holotype.

Etymology: from the umbilicate shell form.

Occurrence: Haywood Landing Member, Belgrade Formation, North Carolina; Kirkwood Formation, Delaware.

Figured specimens: Fig. 1, USNM 488706 (holotype). Fig. 2, USNM 488707 (paratype A). Fig. 3, USNM 488708 (paratype B). Fig. 4, Fulton Collection (paratype C). Fig. 5, USNM 488709 (paratype D). Other occurrence: locality 91LW53, near Dover, Kent County, Delaware (Virginia Museum of Natural History Coll.).

Discussion: Comparisons of *Fenolignum*

umbilicatum to other superficially similar ocenebrines are given under the discussion for the genus. In addition to the Silverdale specimens from the Haywood Landing Member of the Belgrade Formation, L.W. Ward has collected several poorly preserved examples (in the collections of the Virginia Museum of Natural History) from an outcrop he assigns to the Kirkwood Formation. This occurrence in Delaware is somewhat younger than that in the Haywood Landing Member. Sugarman *et al.* (1993) have dated the Kirkwood Formation as Burdigalian (late Early Miocene), which would make this formation comparable in age to the Chipola Formation of Florida. Based on the occurrence of the diatom *Actinoptychus heliopelta,* Ward (in press) correlates the Kirkwood Formation in its type area at Shiloh, New Jersey, and in its Delaware outcrop, with his "bed 3-A" (Ward, 1992, p. 6) near the base of the Calvert Formation of Maryland.

Genus MIOCENEBRA Vokes, 1963

Miocenebra VOKES, 1963, Tulane Stud. Geol., v. 1, no. 4, p. 162.

Type species: *Tritonalia (Miocenebra) silverdalense* Vokes, 1963, by original designation.

Description: "Shell greatly elongated, spire much elevated, constricted above the shoulder with an appressed suture. Formation of the varices irregular, with one always present at the aperture, although the others may be reduced to strong nodes. Aperture oval, margin complete, outer lip slightly crenulated. Canal elongated and completely closed over to form a tubular structure." (Vokes, 1963)

Discussion: Miocenebra resembles *Ocinebrina* in having a single terminal varix, but the aperture is more like that of *Pteropurpura,* being small and ovate with an entire peristome. *Ocenebrina* has several strong denticles on the inner side of the outer lip, as in *Ceratostoma* and *Ocenebra* but unlike *Miocenebra* (compare pl. 1, fig. 6, with pl. 2, figs. 1, 7). *Miocenebra* is most similar to the European genus *Hadriania,* which shares with *Miocenebra* the unusual anal sulcus as well as the high spire. The American genus differs from *Hadriania* principally in having irregularly placed varix-like axial ribs and in its exceptionally high spire. More material may reveal that *Miocenebra* is an unusual American *Hadriania* that left no descendants beyond the Late Oligocene.

MIOCENEBRA SILVERDALENSIS (Vokes)

Plate 1, figure 6

Tritonalia (Miocenebra) silverdalense VOKES, 1963, Tulane Stud. Geol., v. 1, no. 4, p. 162, pl. 2, figs. 6, 7.

[Miocenebra] silverdalense (Vokes).VOKES, 1971, Bulls. Amer. Paleontology, v. 61, no. 268, p. 126.

Description: "Shell moderate in size, spire greatly elevated, whorls constricted above the shoulder, with an appressed suture that is sinuated by the axial nodes. Six adult whorls, nucleus unknown. Axial sculpture on the early whorls consists of about 12 equal nodes, which gradually diminish to about seven unequal nodes on the body whorl. Of these seven nodes, three are stronger, giving the appearance of varices, but there is no evidence of a break in the shell deposition, so that these are not true varices except at the aperture. Spiral sculpture consists of irregularly alternating weak and strong cords. Each strong cord has a medial groove which separates it into what appears to be two, however, if the shell is worn this groove disappears and the cord seems to be a single wide one. There are perhaps as many as 30 primary spirals on the body whorl and pillar of an adult specimen. Aperture oval, slightly crenulated within the labrum by grooves which correspond to the major external cords. Siphonal canal long, completely closed over by an extension from the columella, to form a tubular structure." (Vokes, 1963)

Holotype: USNM 644380; height 28.5 mm, diameter 12.4 mm.

Type locality: TU 562, Haywood Landing Member, Belgrade Formation (= "Silverdale beds"); Onslow County marl pit, near Silverdale, Onslow County, North Carolina.

Occurrence: Haywood Landing Member, Belgrade Formation, North Carolina.

Figured specimen: USNM 644380 (holotype).

Discussion: We have no additional material and there is nothing that can be added to the original description.

Genus OCINEBRINA Jousseaume, 1880

Ocinebrina JOUSSEAUME, 1880, Le Naturaliste, Année 2, no 42, p. 335; JOUSSEAUME, 1882, Rev. Mag. Zool., (Ser. 3) v. 7, p. 332.

Type species: *"Fusus corallinus"* Scacchi, 1836, by original designation [*Murex corallinus* Scacchi, 1836 = *Murex aciculatus* Lamarck, 1822].

Corallina BUCQUOY, DAUTZENBERG, and DOLLFUS, 1882, Moll. Mar. Roussilon, v. 1, p. 24.

Type species: *Murex aciculatus* Lamarck, 1822, by original designation.

Ocenebrina COSSMANN, 1903, Essais Paléoconch. Comp., v. 5, p. 38. Emendation.

Dentocenebra MONTEROSATO, 1917, Boll. Soc. Zool. Ital., (Ser. 3) v. 4, p. 21.

Type species: *Murex edwardsi* (Payraudeau, 1826), by subsequent designation, Lamy, 1919.

Description: "Shell with rather elevated conical spire, whorls ornamented by numerous longitudinal ribs, cut by circular striae, aperture oval with columellar margin appressed and much less curved than the outer margin, the latter internally denticulate; canal very short and closed anteriorly." (Jousseaume, 1882, p. 332, *translated*)

Discussion: Vokes (1971, p. 8) considered *Ocinebrina* as a subgenus of *Ocenebra,* but studies of egg capsules (D'Asaro, 1991) reveal marked differences between the two groups, implying that *Ocenebra* and *Ocinebrina* are not closely related. Shell characters further support this distinction. Species of *Ocinebrina* lack true varices, their axial sculpture consisting instead of rounded scaly ribs. The outer lip forms a terminal varix in the adult, and is thickened on its inner side by a deeply recessed ridge, which bears about six denticles. In some individuals of the type species, *O. aciculata* (Lamarck, 1822), the lowermost of the nine spiral cords on the body whorl above the canal is slightly extended as a short, blunt labral tooth. In the Pliocene Mediterranean *O. scalaris* (Brocchi, 1814), the entire lower sector of the outer lip may be extended ventrally as a lobe. These features do not occur in the Recent Mediterranean *O. edwardsi* (Payraudeau, 1826) or in the several Recent northeastern Pacific species, such as *O. gracillima* (Stearns, 1872), *O. interfossa* (Carpenter, 1864), and *O. lurida*

PLATE 2

Figures Page

1-5. *Ocinebrina francesae*, n. sp. 78
1. (X 3) NMB H-17656 (holotype); height 15.7 mm, diameter 10.8 mm.
Locality: NMB 17516, Paraguaná Peninsula, Falcón State, Venezuela (= TU 1269); Cantaure Formation.
2. (X 3) NMB H-17657 (paratype A); height 14.2 mm, diameter 9.6 mm.
3. (X 3) NMB H-17665 (paratype B); height 17.8 mm, diameter 12.0 mm.
4. (X 3) NMB H-17666-1 (paratype C); height 17.0 mm, diameter 11.5 mm.
5. (X 3 1/2) NMB H-17666-2 (paratype D); height 12.0 mm, diameter 7.1 mm.
Locality of all: same as holotype.

6. *Ocinebrina sublavata* (Basterot) 79
(X 2) NMB H-17658; height 23.6 mm, diameter 14.5 mm.
Locality: Saucats, France; Middle Miocene.

7. *Argyrobessa kellumi* (Richards) 79
(X 1 1/4) ANSP 15838 (holotype); height 42.5 mm, diameter 25.0 mm.
Locality: Gillette's marl pit, Silverdale, North Carolina; Haywood Landing Member, Belgrade Formation.

8. *Ceratostoma rorifluum* (Adams and Reeve) 79
(X 1 1/2) USNM 880169; height 33.3 mm, diameter 18.0 mm.
Locality: Katsuura, Japan; Recent.

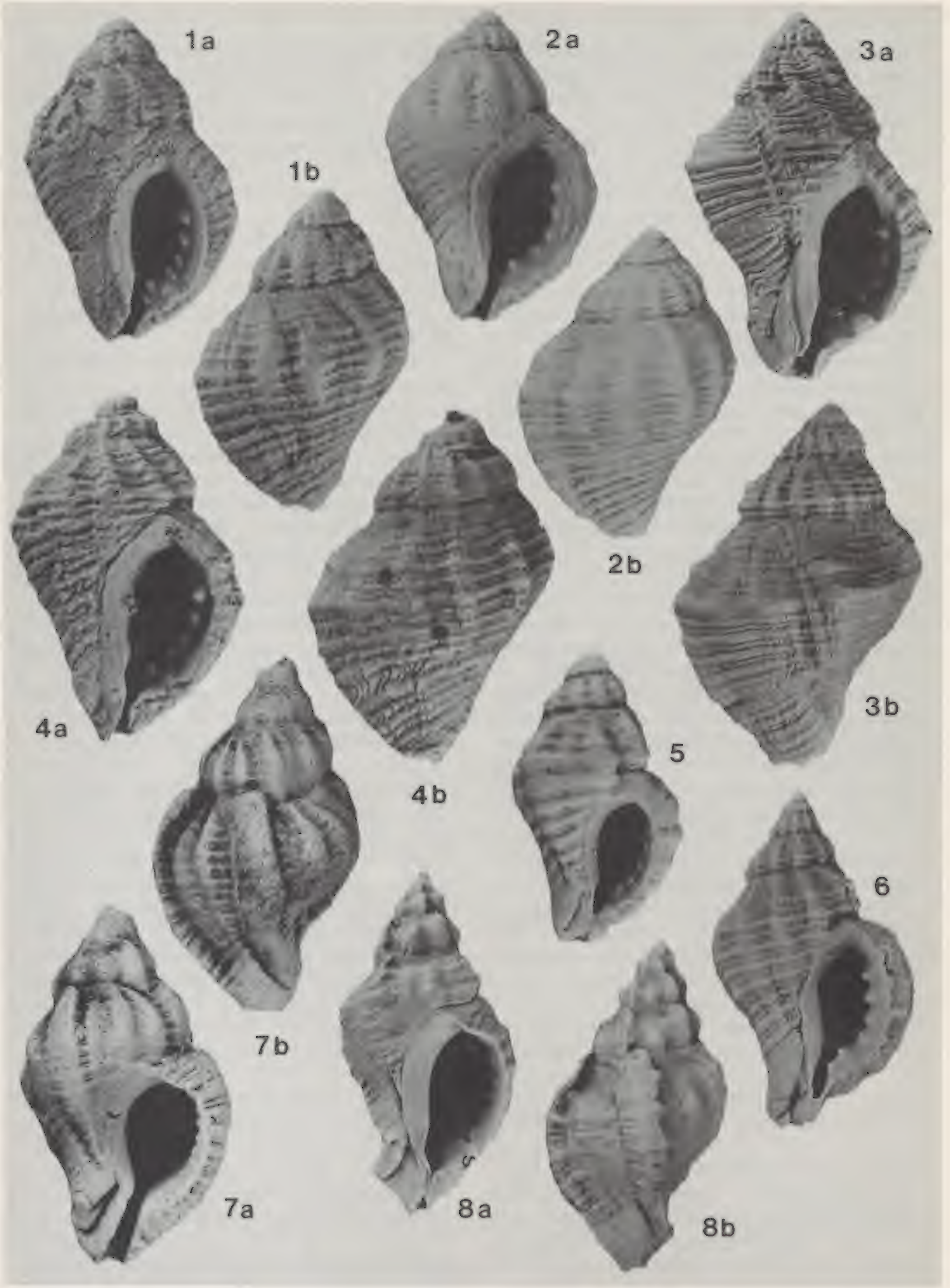

PLATE 2

(Middendorff, 1848), which have been assigned to *Ocenebra* by most previous authors but which McLean (1996) has transferred to *Ocinebrina.*

The discovery of *Ocinebrina francesae*, n. sp., from the Early Miocene Cantaure Formation of Venezuela, fills a wide biogeographical gap between the eastern Atlantic and northeastern Pacific members of the genus. Given that *Ocinebrina* is one of the oldest known genera of the Ocenebrinae, being represented in Europe by the Eocene species *O. bicostata* (Deshayes, 1835), it is likely that *O. francesae* represents a westward expansion of the genus, and that the temperate northeastern Pacific members are derived from this Atlantic group.

OCINEBRINA FRANCESAE
Gibson Smith and Gibson Smith MS, n. sp.
Plate 2, figures 1-5

Description: Shell broadly biconic, with four teleoconch whorls, and a protoconch of about two and one-half smooth, bulbous whorls, line of demarcation between protoconch and onset of teleoconch ornamentation imprecise. Outer shell surface translucent tan calcite, inner layer creamy white aragonite, resulting in decortication of surface on most examples. Axial ornamentation on earliest ornamented whorls of about 15 low ridges, gradually diminishing to nine on body whorl. Axial ribs best developed at periphery, varying greatly in strength from almost invisible to strongly angulate, the latter resulting from strong spiral cord running between axials. Numerous axial growth lamellae giving a fimbriate appearance to area between spiral cords. Usually only terminal varix thickened, but on some individuals from three to five additional varices developed on body whorl. Spiral ornamentation of about 16 low rounded cords on body whorl and siphonal canal. Of these, four on body whorl portion slightly stronger. On penultimate and earlier whorls intersection of axial ridges and spiral cords giving a cancellate appearance; on body whorl spiral ornamentation dominating. Suture shallow, resulting in a globular appearance for the shell. Aperture large, oval; inner lip smooth, appressed along entire length; outer lip patulous, with five (rarely six) strong denticles. On well-preserved specimens, at margin of aperture between first and second anterior denticles, a small labral tooth formed at end of spiral cord, enlarged only on adapertural side of terminal varix. Siphonal canal short, broad, sealed over by an extension of the columellar wall.

Holotype: NMB H-17656; height 15.7 mm, diameter 10.8 mm.

Type locality: NMB 17516, Cantaure Formation (lower beds); Paraguaná Peninsula, Falcón State, Venezuela (= TU 1269).

Paratype A: NMB H-17657; height 14.2 mm, diameter 9.6 mm.

Paratype B: NMB H-17665; height 17.8 mm, diameter 12.0 mm.

Paratype C: NMB H-17666-1; height 17.0 mm, diameter 11.5 mm.

Paratype D: NMB H-17666-2; height 12.0 mm, diameter 7.1 mm.

Locality of all, same as holotype.

Etymology of name: For Frances Gibson Smith, of Battersea, London, England, daughter of Mr. and Mrs. Jack Gibson Smith, Surrey, England, the collectors.

Occurrence: Cantaure Formation, Venezuela.

Figured specimens: Fig. 1, NMB H-17656 (holotype). Fig. 2, NMB H-17657 (paratype A). Fig. 3, NMB H-17665 (paratype B). Fig. 4, NMB H-17666-1 (paratype C). Fig. 5, NMB H-17666-2 (paratype D).

Discussion: In the collections from the Cantaure Formation, Paraguaná Peninsula, Venezuela, made by Mr. and Mrs. J. Gibson Smith, formerly of Caracas, there are over 100 specimens of an undescribed species of *Ocinebrina*. The original collectors long ago recognized this species as new and they intended to name it *"francesae,"* in honor of their daughter Frances, who collected many of the specimens in the type lot. The Gibson Smith Collection is now at the Naturhistorisches Museum, Basel, Switzerland, and we are pleased to be able to include their new taxon herein.

This species is similar to the northeastern Pacific species *O. lurida* (Middendorff, 1848) in that the closure of the canal is very slight if at all. Most specimens of *O. francesae* (which are extremely "beach-worn") have an open canal; however, one paratype (pl. 2, fig. 5) does have traces of closure, indicating that *Ocinebrina* is the proper place for the form, the only species

of this genus in the western Atlantic.

Although all species of *Ocinebrina* are frustratingly similar, *O. francesae* is perhaps most like *O. sublavata* (Basterot, 1825), a common Early and Middle Miocene species from France (pl. 2, fig. 6), which has a somewhat more extended siphonal canal.

Genus ARGYROBESSA, n. gen.

Type species: *Murex kellumi* Richards, 1943.

Description: Fusiform ocenebrine with trivaricate teleoconch whorls; between each pair of varices two to four axial ribs extending to the base of the canal; varices crossed by about eight spiral cords on last whorl; outer lip crenulate, planar, without labral tooth; inner side of outer lip with ten denticles; inner lip adherent along entire length; umbilical slit present. Siphonal canal open in unique specimen, possibly closed in well-preserved material.

Etymology: argyros (Greek: silver) and *bessa* (Greek: a wooded glen), for the Silverdale beds (Haywood Landing Member of the Belgrade Formation), the stratum from which the type species was described.

Discussion: Vokes (1964, p. 23) suggested that *Murex kellumi* Richards, 1943, from the Late Oligocene "Silverdale beds" [= Haywood Landing Member of the Belgrade Formation] of North Carolina, be placed in the genus *Ceratostoma*. Although the shell of the single available specimen is worn, it differs markedly from *Ceratostoma* by the absence of a labral tooth, by possibly having an open, rather than a sealed, siphonal canal, and by having two to four long intervarical ribs, instead of one intervarical node between adjacent varices. No other ocenebrine is at all similar to *Murex kellumi*. For this reason we propose the new genus *Argyrobessa* to accommodate it. The most similar living species of *Ceratostoma* is the Japanese *C. rorifluum* (Adams and Reeve, 1849), which differs by having four varices, a single intervarical rib between varices, and a closed canal (see pl. 2, fig. 8).

As originally noted by Richards (1943, p. 524), *Argyrobessa kellumi* superficially resembles species assigned to the muricine genus *Chicoreus* sensu lato. Richards (1943) compared *A. kellumi* to a species from the Dominican Republic that was then undescribed, but which was subsequently named *Chicoreus (Chicoreus) dujardinoides* (Vokes, 1963) (see Vokes, 1989a, p. 35, plate 2, fig. 11). *Argyrobessa kellumi* also closely resembles the Recent Indo-West Pacific *Chicoreus (Rhizophorimurex) capucinus* (Lamarck, 1822) in lacking spines and in having two or three intervarical ribs. Species of *Chicoreus* s.l. differ from *Argyrobessa* by having a lirate rather than denticulate outer lip, by the presence of a parietal rib at the apical end of the inner lip, and by having shorter intervarical ribs or nodes, rather than long ribs that extend to the base.

ARGYROBESSA KELLUMI (Richards)
Plate 2, figure 7

Murex kellumi RICHARDS, 1943, Jour. Paleontology, v. 17, p. 524, pl. 85, figs. 3, 4.

[Ceratostoma] kellumi (Richards). VOKES, 1964, Malacologia, v. 2, no. 1, p. 23; VOKES, 1971, Bulls. Amer. Paleontology, v. 61, no. 268, p. 62.

Description: "Shell subfusiform, five whorls, three varices, two to four ribs between the varices. Revolving lines prominent. Primary concentric ridges are separated from each other by two narrow grooves. Aperture suboval, with canal slightly deflected to the left. Ten aperture teeth. Conspicuous groove to the left of the canal." (Richards, 1943)

Holotype: ANSP 15838; height 42.5 mm, diameter 25.0 mm.

Type locality: Haywood Landing Member, Belgrade Formation; Gillette's marl pit, on the left side of Webbs Creek, half a mile southeast of Silverdale, Onslow County, North Carolina.

Occurrence: Haywood Landing Member, Belgrade Formation, North Carolina.

Figured specimen: ANSP 15838 (holotype).

Discussion: Unfortunately, no specimens of *A. kellumi* have come to light since Richards (1943) described the species on the basis of a single worn shell.

Genus CERATOSTOMA Herrmannsen, 1846

Cerostoma CONRAD, 1837, Acad. Nat. Sci. Philadelphia, Jour., v. 7, p. 263.

Type species: *Murex (Cerostoma) nuttalli* Conrad, 1837, by monotypy.

Ceratostoma HERRMANNSEN, 1846, Indicis Generum Malacoz., v. 1, p. 206. New name for *Cerostoma* Conrad, 1837, *non* Latreille, 1802.

Spinostoma COEN, 1943, Acta Pont. Acad. Sci., v. 11, p. 90.

Type species: *Murex nuttalli* Conrad, 1837, by subsequent designation, Vokes, 1964.

Description: "Shell as in the genus *Murex*; labrum with an erect tooth as in *Monoceros*." (Conrad, 1837)

Discussion: The name *Ceratostoma* has been used for a variety of trivaricate ocenebrines possessing a labral tooth. Here we restrict *Ceratostoma* to ocenebrines with three or four varices on the body whorl, cancellate sculpture on early teleoconch whorls, a single intervarical node between adjacent varices, and spiral sculpture consisting of strong cords, three to seven of which cross each intervarical node. The anterior siphonal canal is closed in the adult, and the inner side of the outer lip usually bears denticles. The labral tooth is formed at the end of a spiral groove below the intervarical nodes. The outer lip is erect, as is the basal sector of the inner lip in most species. There is no umbilical slit.

The genus *Pteropurpura* is similar to *Ceratostoma* in having a trivaricate shell in which the early teleoconch whorls bear a cancellate sculpture. It differs from *Ceratostoma* by having a much smaller aperture and by lacking a labral tooth.

Living species of *Ceratostoma* are confined to the temperate northeastern and northwestern Pacific. During the Early to Middle Miocene, however, the genus was also represented in Europe and in eastern North America; and a Pliocene species (*C. notiale*) was described by Vokes (1988) from the Esmeraldas beds of Ecuador. *Ceratostoma*, therefore, represents an intriguing example of a group that became regionally extinct in tropical waters and in the Atlantic Ocean but that survives in the temperate North Pacific.

CERATOSTOMA VIRGINIAE (Maury)

Plate 3, figures 1, 2

Murex virginiae MAURY, 1910, Bulls. Amer. Paleontology, v. 4, no. 21, p. 25(143), pl. 6(23), fig. 5.

Pteropurpura virginiae (Maury). GARDNER, 1947, U.S. Geol. Survey, Prof. Paper 142-H, p. 525.

[Pteropurpura] virginiae (Maury). VOKES, 1971, Bulls. Amer. Paleontology, v. 61, no. 268, p. 116.

Description: "Shell small with some resemblance to *Typhis*, trigonal, biconic; whorls six; the two later being sharply carinated at the shoulders. Varices six, the alternate three being much more pronounced and giving the shell its triangular form. Spiral sculpture of raised threads which on the last whorl alternate with one or two finer, intercalated lines. Fainter, longitudinal threads form with the spirals a fine cancellation on the last whorl. Aperture oval, slightly more than half the length of the shell; canal narrow, reflexed." (Maury, 1910)

Holotype: PRI 3460; height 15.0 mm, diameter 8.0 mm.

Type locality: Chipola Formation; "Bailey's Ferry, Florida."

Occurrence: Chipola Formation, Florida.

Figured specimens: Fig. 1, USNM 488710; height 19.3 mm, diameter 11.8 mm; locality TU 830. Fig. 2, USNM 488711; height 18.7 mm, diameter 11.1 mm; locality TU 830. Other occurrences: TU localities 457, 458, 459, 546 (common), 547, 548, 549, 554, 555, 708, 787, 806, 807, 817, 818, 819, 820, 821, 823, 824, 825, 828, 830 (common), 831, 949, 950, 951, 998, 999, 1021, 1048, 1050, 1196.

Discussion: In 1971 Vokes referred this common Chipola species to the genus *Pteropurpura* because most of the examples do not have the labral tooth preserved and the fimbriate shell is much like that of species of *Pteropurpura*. However, in rare examples this tooth is developed (see pl. 3, fig. 2c) and, even without the labral tooth present, the open denticulate aperture is more typical of *Ceratostoma* than *Pteropurpura*. This species also has the early whorls with a finely cancellate sculpture in contrast to the lamellar varices seen in the other species heretofore attributed to *Ceratostoma* in the western Atlantic. These others are now placed in

Pterorytis (Microrhytis) below, leaving *C. virginiae* as the only valid representative of the genus *Ceratostoma* in the area.

The holotype is a small specimen, our largest example (TU 546) measures 22.5 mm in height.

Genus PTEROPURPURA Jousseaume, 1880

Pteropurpura JOUSSEAUME, 1880, Le Naturaliste, Année 2, no. 42, p. 345; JOUSSEAUME, 1882, Rev. Mag. Zool., (Ser. 3) v. 7, p. 334.

Type species: *Murex macropterus* Deshayes, 1839, by original designation.

Centrifuga GRANT and GALE, 1931, San Diego Soc. Nat. Hist., Mem., v. 1, p. 706.

Type species: *Murex centrifuga* Hinds, 1844, by original designation.

Shaskyus BURCH and CAMPBELL, 1963, Jour. de Conchyl., v. 103, p. 201.

Type species: *Murex festivus* Hinds, 1844, by original designation.

Description: "Shell with spire elongated to triangular pyramid, whorls ornamented by three wide lamellar varices reaching almost the middle of the canal; aperture small, oval, margins continuous and detached; canal wide at the base, subulate anteriorly." (Jousseaume, 1882, p. 334, *translated*)

Discussion: The genus *Pteropurpura* is characterized by having a trivaricate shell, very small rounded to broadly ovate aperture, erect outer and inner apertural lips, and a closed canal. The varices on adjacent whorls usually do not form connecting buttresses across the suture as they do in *Jaton*. There is no labral tooth. Spiral sculpture usually consists of fine cords or threads, which in some species are obsolete.

The Californian *Murex festivus* Hinds, 1844, has been made type of the genus *Shaskyus*, but we regard the distinction between *Shaskyus* and *Pteropurpura* as minor. *Pteropurpura festiva* differs from other species of the subgenus by having abaperturally recurved, instead of erect, alate varices, and by having the varices on adjacent whorls touching in a buttress-like fashion (see pl. 3, fig. 4). The Californian *P. vokesae* Emerson, 1964 (*n.n. pro Murex rhyssus* Dall, 1919, *non M. rhysus* Tate, 1888) is morphologically intermediate between *P. festiva* and the other northeastern Pacific species of *Pteropurpura*.

M. Smith (1940, p. 244, pl. 2, fig. 3; holotype UF 174297) named *Murex gaza* from the Gulf of Mexico. Sunderland and Sunderland (1994, p. 14) have figured the holotype and we believe that this specimen is only a juvenile *Pteropurpura festiva*, and the locality given for *M. gaza* is erroneous (see pl. 3, fig. 5).

The presence of labral denticles is an inconsistent character in the genus *Pteropurpura*. In the type species of the genus, *P. macropterus* (Deshayes), the inner side of the outer lip is usually smooth, but occasional specimens have small denticles. Two other eastern Pacific species, *P. festiva* and *P. erinaceoides* (Valenciennes, 1832), sometimes have these denticles (pl. 3, fig. 4a). The three fossil and Recent western Atlantic species considered below have five denticles on the inner side of the outer lip (pl. 4, figs. 2c, 4a). These denticles are much smaller than those in *Ceratostoma*. As in other species of *Pteropurpura*, the aperture of the Atlantic species is small and rounded instead of large and markedly ovate as in *Ceratostoma*.

The genus *Pteropurpura* is represented in Recent seas by species in West Africa, the western Atlantic, tropical eastern Pacific, and warm-temperate northeastern and northwestern Pacific. The oldest member of the genus is *P. delbosiana* (Grateloup, 1847), from the Burdigalian (Early Miocene) of southwestern France. In the New World, the genus is first represented by *P. boesei*, n. sp., from the probably Late Miocene Santa Rosa beds, Veracruz, Mexico (see below). All Pacific records of *Pteropurpura* are from the Pliocene or younger. The genus *Poropteron* Jousseaume, 1880, comprises a related group of six species from southern Africa and the island of St. Helena, distinguished by having an adapically and ventrally curving spine at the posterior end of the varices. We separate as *Odontopurpura*, n. subgen., a species of *Pteropurpura, P. festivoidea* (Vokes, 1963), characterized by a labral tooth formed as the

extension of a spiral cord. It is possible that this species is not closely related to other species of *Pteropurpura*.

Subgenus PTEROPURPURA s.s.
PTEROPURPURA (PTEROPURPURA) BOESEI, n. sp.
Plate 4, figure 1

Pteropurpura aguilari (Böse). PERRILLIAT, 1972, Paleontología Mexicana, no. 32, p. 81, pl. 40, figs. 5-10 (*not* of Böse).

Description: Shell with seven teleoconch whorls, protoconch lacking in type material. Shell composed of two layers: a translucent outer calcitic layer and a creamy aragonitic inner layer. Earliest whorls decorticated; axial ornamentation on first decorated whorl of 12 small lamellar flanges, gradually gaining in strength and reducing in number to six per whorl. On about sixth teleoconch whorl every other flange disappearing to leave three varices and three heavy, rounded intervarical nodes per whorl. Varices thick at base, composed of a single lamina of shell material on abapertural side, but multiple layers on adapertural side, giving a faint fimbriation to varical face. Spiral ornamentation on early teleoconch whorls of two cords; gradually weakening and by fourth teleoconch whorl totally disappearing; visible only on adapertural varical faces as three strong grooves in the fimbriated surface. Suture impressed. Aperture elongate-oval; inner lip smooth, narrow, briefly appressed at posterior end. Inner side of outer lip with five small denticles. Siphonal canal moderately long, narrow, slightly recurved at distal end; completely sealed over by an extension from columellar wall.

Holotype: USNM 283714; height 30.9 mm, diameter 19.0 mm.

Type locality: USGS 23737, Santa Rosa beds; 3 km northeast of Santa Rosa [now Istal], formerly on the Veracruz to Santa Lucretia [now Jesus Carranza] railroad [which now exists only as the highway right-of-way to Istal], Veracruz, Mexico.

Paratype: USNM 350019; height 6.2 mm, diameter 3.9 mm; locality USGS 9995, 3 km northeast of Santa Rosa, Veracruz, Mexico.

Etymology of name: For Emil Böse, in honor of his pioneering work on the Tertiary faunas of Mexico.

Occurrence: Santa Rosa beds, Veracruz, Mexico.

Figured specimen: USNM 283714 (holotype).

Discussion: The three specimens that Perrilliat figured from the Santa Rosa fauna as *P. aguilari* Böse are not that species but are a more inflated shell with three strong folds on the apertural face of the varix. The smallest specimen (USNM 350019) that Perrilliat figured (1972, pl. 40, figs. 9, 10) shows well the cancellate early whorls typical of *Pteropurpura*.

The material from Santa Rosa was originally collected by Bruce Wade in 1920. Part of the collection went to the U.S. National Museum and was given the locality number 9995 and part originally went

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PLATE 3

Figures Page

1, 2. *Ceratostoma virginiae* (Maury) 80
1. (X 3) USNM 488710; height 19.3 mm, diameter 11.8 mm.
2. (X 3) USNM 488711; height 18.7 mm, diameter 11.1 mm.
Locality of both: TU 830, Chipola Formation.

3. *Pteropurpura (Odontopurpura) festivoidea* (Vokes) 87
(X 2 1/2) USNM 644379 (holotype); height (incomplete) 24.0 mm, diameter 14.0 mm.
Locality: TU 562; Haywood Landing Member, Belgrade Formation.

4, 5. *Pteropurpura (Pteropurpura) festiva* (Hinds) 81
4. (X 1 1/4) USNM 880167; height 50.8 mm, diameter 25.7 mm.
Locality: Stearn's Wharf, Santa Barbara, California, 5 meters; Recent.
5. (X 2) USNM 880168; height 27.9 mm, diameter 14.0 mm.
Locality: 160 km southwest of San Diego, California; Recent.

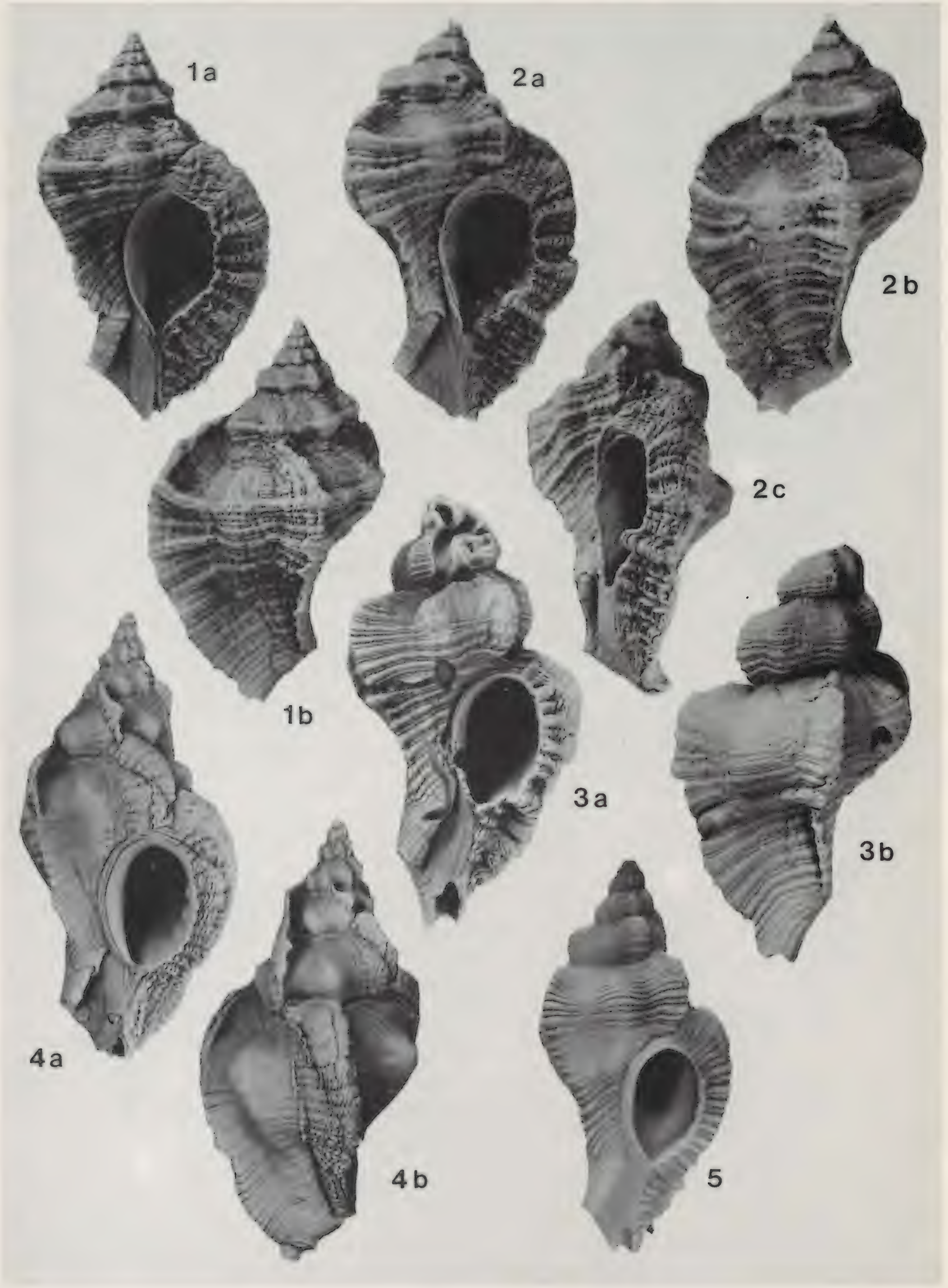


PLATE 3

to the Johns Hopkins University Collections. Subsequently, this material also was placed in the U.S. National Museum and given the locality number 23723. As was discussed in Vokes (1994, p. 138) this remarkable locality, thought to be of Late Miocene age, has never been located and is assumed to be buried by subsequent soil erosion. Like the shell bed at Bowden, Jamaica, to which it is similar, Santa Rosa probably represents a gravity-flow of shallow-water material into deeper water and, also like the Bowden shell bed, was a very restricted outcrop.

PTEROPURPURA (PTEROPURPURA) AGUILARI (Böse)

Plate 4, figures 2, 3

Murex (Pteropurpura) aguilari BÖSE, 1910, Jahr. K.K. Geol. Reichsanst., v. 60, p. 233, pl. 12, fig. 11; TOULA, *ibid.*, p. 262.

[Pteropurpura] aguilari (Böse). VOKES, 1971, Bulls. Amer. Paleontology, v. 61, no. 268, p. 14.

Not *Pteropurpura aguilari* (Böse). PERRILLIAT, 1972, Paleontología Mexicana, no. 32, p. 81, pl. 40, figs. 5-10 [= *P. boesei*, n. sp.].

Description: Shell with seven teleoconch whorls, and a protoconch of from one and one-half to two and one-half smooth, bulbous whorls (exact line of demarcation uncertain due to shell decortication). Shell composed of two layers, a translucent outer calcitic layer, easily decorticated, and a creamy aragonitic inner layer. Axial ornamentation on first decorated whorl of 12 small lamellar flanges, gradually reducing in number but gaining in strength, about fourth teleoconch whorl only three strong wing-like varices remaining, with one large intervarical node between each pair. Varices composed of a single lamina of shell material on abapertural side, but multiple layers on adapertural side, giving a faint fimbriation to varical face. Spiral ornamentation on early teleoconch whorls of three cords, one at shoulder and two anterior to it. Spiral cords persisting up to about fourth teleoconch whorl, disappearing at about same place as the multiple varical laminae. Last three teleoconch whorls almost completely smooth, only a hint of presence of former cords on varical face, primarily at shoulder. Suture deeply impressed. Aperture elongate-oval; inner lip smooth, narrow, briefly appressed at posterior end. Inner side of outer lip with five small denticles. Siphonal canal moderately long, narrow, slightly recurved at distal end; completely sealed over by an extension from columellar wall.

Holotype: Unknown; height 26.8 mm, diameter 13 mm (*fide* Bosë, 1910, p. 234).

Type locality: Concepcion Inferior Formation; Kilometer 70 on the Tehuantepec Railroad [5 km north of Almagres, Veracruz, Mexico] (= TU 1321).

Occurrence: Concepcion Inferior Formation, Veracruz, Mexico.

Figured specimens: Fig. 2, UCMP 39881; height 30.3 mm, diameter 18.8 mm; locality UCMP S-2647, Texistepec, Veracruz, Mexico.

PLATE 4

Figures — Page

1. *Pteropurpura (Pteropurpura) boesei*, n. sp 82
   (X 2) USNM 283714 (holotype); height 30.9 mm, diameter 19.0 mm.
   Locality: USGS 23737, 3 km northeast of Santa Rosa, Veracruz, Mexico; Santa Rosa beds.

2, 3. *Pteropurpura (Pteropurpura) aguilari* (Böse) 84
   2. (X 2) UCMP 39881; height 30.3 mm, diameter 18.8 mm.
      Locality: UCMP S-2647, Texistepec, Veracruz, Mexico; Concepcion Inferior Formation.
   3. (X 2) UCMP 39882; height 21.7 mm, diameter 13.5 mm.
      Locality: UCMP S-4276 [no data available]; Concepcion Inferior Formation.

4, 5. *Pteropurpura (Pteropurpura) bequaerti* (Clench and Pérez Farfante) 86
   4. (X 1 1/2) USNM 488712; height 42.6 mm, diameter 22.8 mm.
      Locality: TU 977; Late Pleistocene.
   5. (X 3) USNM 880170; height 19.3 mm, diameter 10.4 mm.
      Locality: off Anna Maria Key, Florida, in 40 meters; Recent.

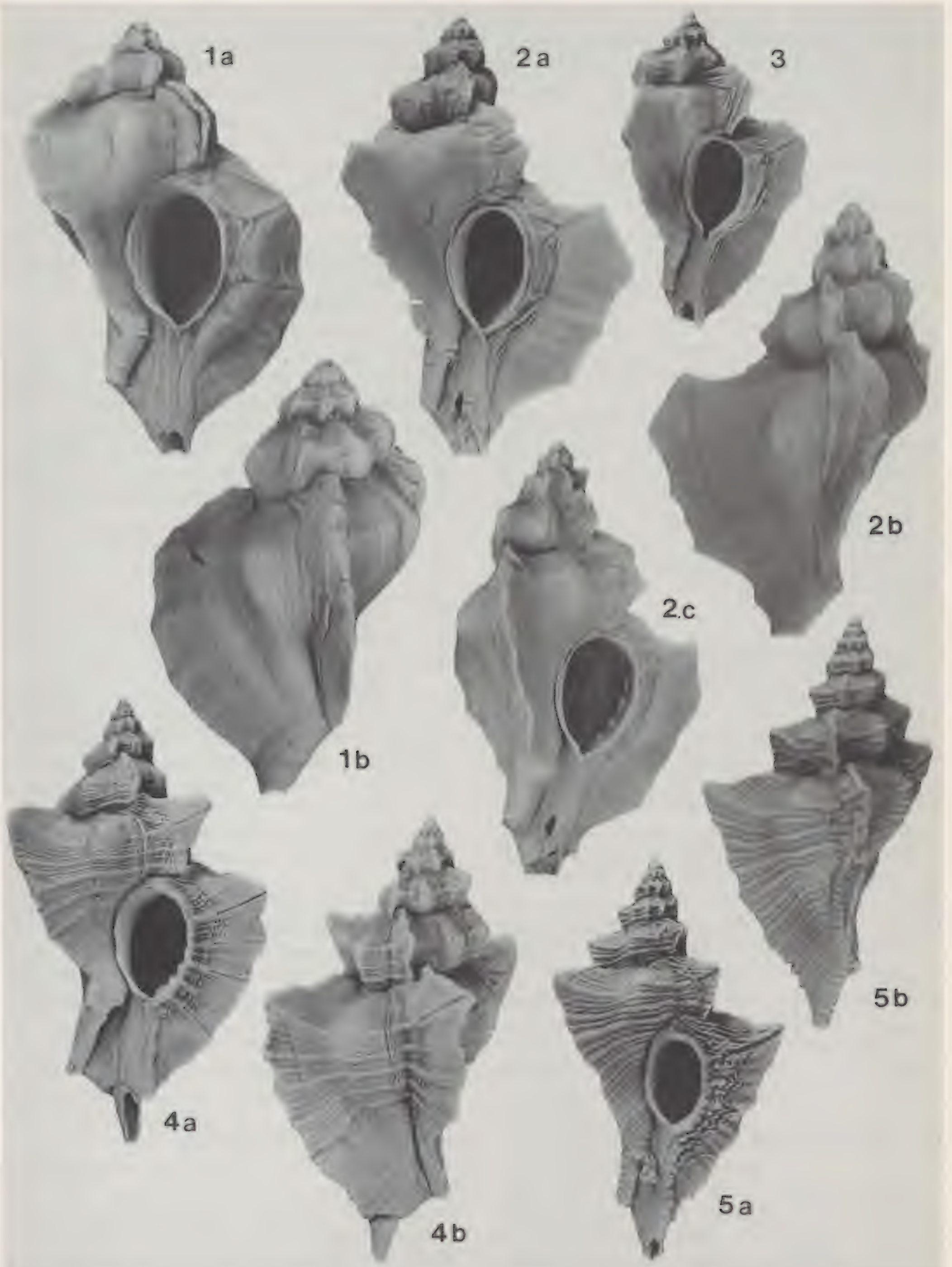


PLATE 4

Fig. 3, UCMP 39882; height 21.7 mm, diameter 13.5 mm; locality UCMP S-4276 [Veracruz, Mexico; no data available]. Other occurrences: TU localities 1025, 1318, 1514, 1515.

Discussion: Originally named from the famous "Kilometer 70" locality on the Isthmus of Tehuantepec Railroad, we now have several examples of this species from the Concepcion Inferior Formation in the Isthmus of Tehuantepec. The beds of the Concepcion Inferior have been dated as Neogene Zone N.19, Early Pliocene in age, and are thought to represent deposition in depths of 180-200 meters (Kohl, 1985, p. 25).

Böse's original description (1910, p. 233, pl. 12, fig. 11), based upon the broken holotype, is not very diagnostic but his excellent illustration leaves no question as to the identity of this species, which differs from *P. bequaerti* in having a much smoother shell in contrast to the elaborate surface ornamentation of the younger species.

PTEROPURPURA (PTEROPURPURA) BEQUAERTI (Clench and Pérez Farfante)

Plate 4, figures 4, 5

Murex (Pteronotus) macropterus Deshayes. DALL, 1889, Harvard Mus. Comp. Zool., Bull., v. 18, p. 201; M. SMITH, 1939, Illus. Cat. Recent Species Rock Shells, p. 5, pl. 11, fig. 8 (*not* of Deshayes).

Murex (Pteropurpura) bequaerti CLENCH and PÉREZ FARFANTE, 1945, Johnsonia, v. 1, no. 17, p. 40, pl. 21, figs. 1, 2.

Murex (Pterynotus Sect. *Pteropurpura) bequaerti* Clench and Pérez Farfante. ABBOTT, 1954, Amer. Seashells, p. 205.

[Pteropurpura] bequaerti (Clench and Pérez Farfante). VOKES, 1971, Bulls. Amer. Paleontology, v. 61, no. 268, p. 23.

Pteropurpura bequaerti (Clench and Pérez Farfante). ABBOTT, 1974, Amer. Seashells, Second Ed., p. 177, fig. 1868; RADWIN and D'ATTILIO, 1976, Murex Shells of the World, p. 129, pl. 22, fig. 1; FAIR, 1976, The Murex Book, p. 25, pl. 22, fig. 344; KAICHER, 1980, Card Cat. World-wide Shells, Pack no. 25, Muricidae (Part V), card no. 2513; ABBOTT and DANCE, 1982, Compendium of Seashells, p. 141 (color figure); D'ATTILIO and MYERS, 1983, Festivus, v. 15, no. 3, p. 33, figs. 1-7 [fig. 3, protoconch; fig. 4, operculum; fig. 5, radula]; SUNDERLAND and SUNDERLAND, 1994, Amer. Conchologist, v. 22, no. 1, p. 14 (holotype).

Pteropurpura (Pteropurpura) bequaerti (Clench and Pérez Farfante). VOKES, 1984, Shells and Sea Life, v. 16, no. 11, p. 214, back cover (color figure).

Description: "Shell from 17 to 37 mm (about three-fourths to one and one-half inches) in length, solid and provided with three strong, wing-like varices. Whorls about seven and rather strongly convex. Color a dull white with irregular areas of cream on the base of the varices and on the intervarical ridges. Spire extended. Suture rather deeply impressed. Aperture small, oval, and entire, notched slightly above the opening to the siphonal canal. Both parietal and palatal lips are thin and erect. Siphonal canal short, broad and completely inclosed, with the distal end turned slightly toward the right. Previous siphonal canals exist as very short scales. Axial sculpture consists of three wing-like varices which are broad at the base and knife-like at the outer edge. The front surface of the varices consists of many very low laminae, which are built forward in overlapping layers. There is a single knot-like ridge between the varices. Spiral sculpture consists of numerous, large and small alternating threads. This sculpture passes over the intervarical ridges and up on the back surface of the varices. Postnuclear whorls similar to the later whorls. Periostracum absent." (Clench and Pérez Farfante, 1945)

Holotype: UF 11986; height 25 mm, diameter 15.5 mm (*fide* Clench and Pérez Farfante, 1945, p. 40).

Type locality: Off Delray Beach, Palm Beach County, Florida, in 80 fathoms [146 meters]; collected by F.B. Lyman.

Occurrence: Late Pleistocene and Recent, Gulf of Mexico to North Carolina.

Figured specimens: Fig. 4, USNM 488712; height 42.6 mm, diameter 22.8 mm; locality TU 977. Fig. 5, USNM 880170; height 19.3 mm, diameter 10.4 mm; locality, off Anna Maria Key, Florida, in 40 meters.

Discussion: Although Clench and Pérez Farfante do not note it in the original description, *P. bequaerti*, as well as the earlier western Atlantic species, bears five

small denticles on the inner side of the outer lip (see pl. 4, fig. 4a). The protoconch is of one and one-half rounded whorls and the early teleoconch whorls are strongly cancellate, with initially about twelve lamellae, diminishing to ten and then to six on the third and fourth teleoconch whorls, becoming three varices with three strong intervarical nodes at about the fifth teleoconch whorl. The size is also larger than the original authors realized; some examples measure almost 50 mm.

In the Tulane Collections this species in moderately common in the Late Pleistocene beds from "Mud-Lump 90" off the Mississippi River delta, in beds estimated to have been deposited in 60 meters depth (Morgan *et al.*, 1963, p. 41).

Subgenus ODONTOPURPURA, n. subgen.

Type species: *Tritonalia festivoidea* Vokes, 1963.

Description: Ocenebrine differing from *Pteropurpura* s.s. by the presence of a long intervarical rib between adjacent varices, by the presence of a narrow umbilical slit, and by the presence of a labral tooth at the termination of a basal spiral cord at the edge of the outer lip.

Etymology: Greek prefix *odonto-* referring to tooth, coupled with *Purpura.*

Discussion: Another unusual form found in the Late Oligocene "Silverdale beds" of North Carolina was originally given the specific name *festivoidea* by Vokes (1963) because of the close morphological similarity to *Pteropurpura festiva* (Hinds, 1844), a species living today on the coast of California. Although the Oligocene fossil has three varices and a single intervarical node as in *P. festiva, P.(O.) festivoidea* possesses a strong labral tooth not seen in the living species (compare pl. 3, figs. 3a, 4a).

The eastern Atlantic Miocene to Recent genus *Jaton* is superficially similar to the subgenus *Odontopurpura* in having a trivaricate shell and by virtue of the presence of a labral tooth in the type species, *J. decussatus* (Gmelin, 1791). As in *Odontopurpura*, the labral tooth of *J. decussatus* is formed at the terminus of a spiral cord. However, whereas the cords of *Odontopurpura* are indistinct and weak, those of *Jaton* are broad and prominent. In *Jaton*, the labral tooth arises from a small cord anterior to the second broad primary cord (counting from the shoulder). The intervarical node in *Jaton* is relatively shorter than that in *Odontopurpura*, and is bounded on its apertural side by the shoulder cord (cord 1) and the tooth-bearing cord (cord 2). In *Odontopurpura* the labral tooth arises from the lowest of four cords.

PTEROPURPURA (ODONTOPURPURA) FESTIVOIDEA (Vokes)

Plate 3, figure 3

Tritonalia (Tritonalia) festivoidea VOKES, 1963, Tulane Stud. Geol., v. 1, no. 4, p. 161, pl. 2, fig. 5.

[Ocenebra] festivoidea (Vokes). VOKES, 1971, Bulls. Amer. Paleontology, v. 61, no. 268, p. 121.

Description: "Shell moderate in size, spire elevated, suture deeply constricted giving a much inflated aspect to the individual whorls. Nucleus unknown, about five post-nuclear whorls in the adult. Axial ornamentation consists of three wing-like varices, which are sculptured with minute imbrications on the apertural side. Between each pair of varices is one very strong node. Spiral ornamentation consists of coarse threads alternating with usually three finer threadlets between each pair; about 18 primary threads on the body whorl and pillar. At the juncture of the body whorl and the pillar there is a raised rib which corresponds to an ill-defined anterior apertural tooth and is a conspicuous spiral ridge. Aperture oval, labium distinct, not appressed. Outer margin of the aperture denticulate with about four weak teeth. Canal moderate, slightly recurved, completely roofed over to form a tubular structure typical of *Tritonalia* [= *Ocenebra*]." (Vokes, 1963)

Holotype: USNM 644379; height (incomplete) 24.0 mm, diameter 14.0 mm.

Type locality: TU 562; Haywood Landing Member, Belgrade Formation (= "Silverdale beds"), Onslow County marl pit, near Silverdale, Onslow County, North Carolina.

Occurrence: Haywood Landing Member, Belgrade Formation, North Carolina; Kirkwood Formation, Delaware.

Figured specimen: USNM 644379 (holotype). Other occurrence: locality 92LW22, near Dover, Kent County, Delaware (L.W. Ward Coll.).

Discussion: The holotype of this unusual species is incomplete, as are two additional specimens in the type lot and another two examples collected by L.W. Ward from an outcrop of the Kirkwood Formation near Dover, Delaware. As discussed further under *Fenolignum umbilicatum*, the Delaware specimens are somewhat younger (of late Early Miocene age) than those from the Haywood Landing Member of the Belgrade Formation (Late Oligocene).

Genus PTERORYTIS Conrad, 1863

Pterorytis CONRAD, 1863, Acad. Nat. Sci. Philadelphia, Proc., v. 14, p. 560.

Type species: *Murex umbrifer* Conrad, 1832, by monotypy.

Pterorhytis CONRAD, 1868, Amer. Jour. Conch., v. 4, p. 64. ?Emendation.

Not *Pterorhytis* CONRAD, 1875, Rept. North Carolina Geol. Survey, v. 1, Appendix A, p. 21 [a pelecypod].

Neurarhytis OLSSON and HARBISON, 1953, Acad. Nat. Sci. Philadelphia, Mon. 8, p. 252.

Type species: *"Purpura (Pterorhytis) fluviana"* Dall, 1903, by original designation [= *Pterorhytis fluviana* Dall, 1903].

Description: "Fusiform; six prominent recurved foliated ribs; aperture ovate, channel closed." (Conrad, 1863)

Discussion: The original spelling of this genus by Conrad was as *"Pterorytis,"* without the "h." Subsequently (1868), he spelled it as *Pterorhytis,* and most authors have followed that orthography. Unfortunately, the *Code of Zoological Nomenclature* is explicit on the subject of subsequent spellings and according to Article 32(b) the original spelling is to be preserved unaltered. In addition to the *Pterorytis-Pterorhytis* spellings, there have been numerous other errors, cited in Vokes (1964, p. 22).

It is surprising that, in the original description, Conrad failed to note the single most dramatic character of this genus, the extremely large, projecting labral tooth. The name indicates that to Conrad the most striking characteristic is the sharp fold in the lamellar varices (*ptero* = wing; *rhytis* = fold), formed by the spiral cord at the periphery. The original illustration has no suggestion of a labral tooth, and the specimen does not seem to have had one, as Tuomey and Holmes (1856, p. 141) note: "Mr. Conrad informs us it is but lately that specimens of this shell have been discovered with the erect tooth on the labrum." Presumably, it is one of the latter specimens Conrad illustrated later (1868, pl. 5, fig. 7; refigured here, text-fig. 1), which does show the tooth. Perhaps the Tuomey and Holmes specimen (which is *P. fluviana* Dall) influenced him for, at that time (*ibid.*, p. 63), he re-described *Murex umbrifer* as having four varices, but his specimen has five.

PLATE 5

Figures Page

1-5. *Pterorytis (Pterorytis) umbrifer* (Conrad) 90

1. (X 1 1/4) USNM 488713; height 52.1 mm, diameter 42.0 mm. Locality: TU 613; Yorktown Formation.
2. (X 1 1/2) USNM 488714; height 33.5 mm, diameter 20.5 mm. Locality: Chuckatuck, Virginia (Blow Coll.); Yorktown Formation.
3. (X 1 1/2) USNM 488715; height 37.8 mm, diameter 30.0 mm. Locality: Day's Point, James River, Virginia (Blow Coll.); Yorktown Formation.
4. (X 1 1/2) USNM 488716; height 36.0 mm, diameter 25.4 mm. Locality: Yadkin, City of Chesapeake, Virginia (Campbell Coll.); Yorktown Formation.
5. (X 4, X 10) USNM 488717; height 10.9 mm, diameter 6.0 mm. Locality: Rock Wharf, Smithfield, Virginia (Campbell Coll.); Yorktown Formation.

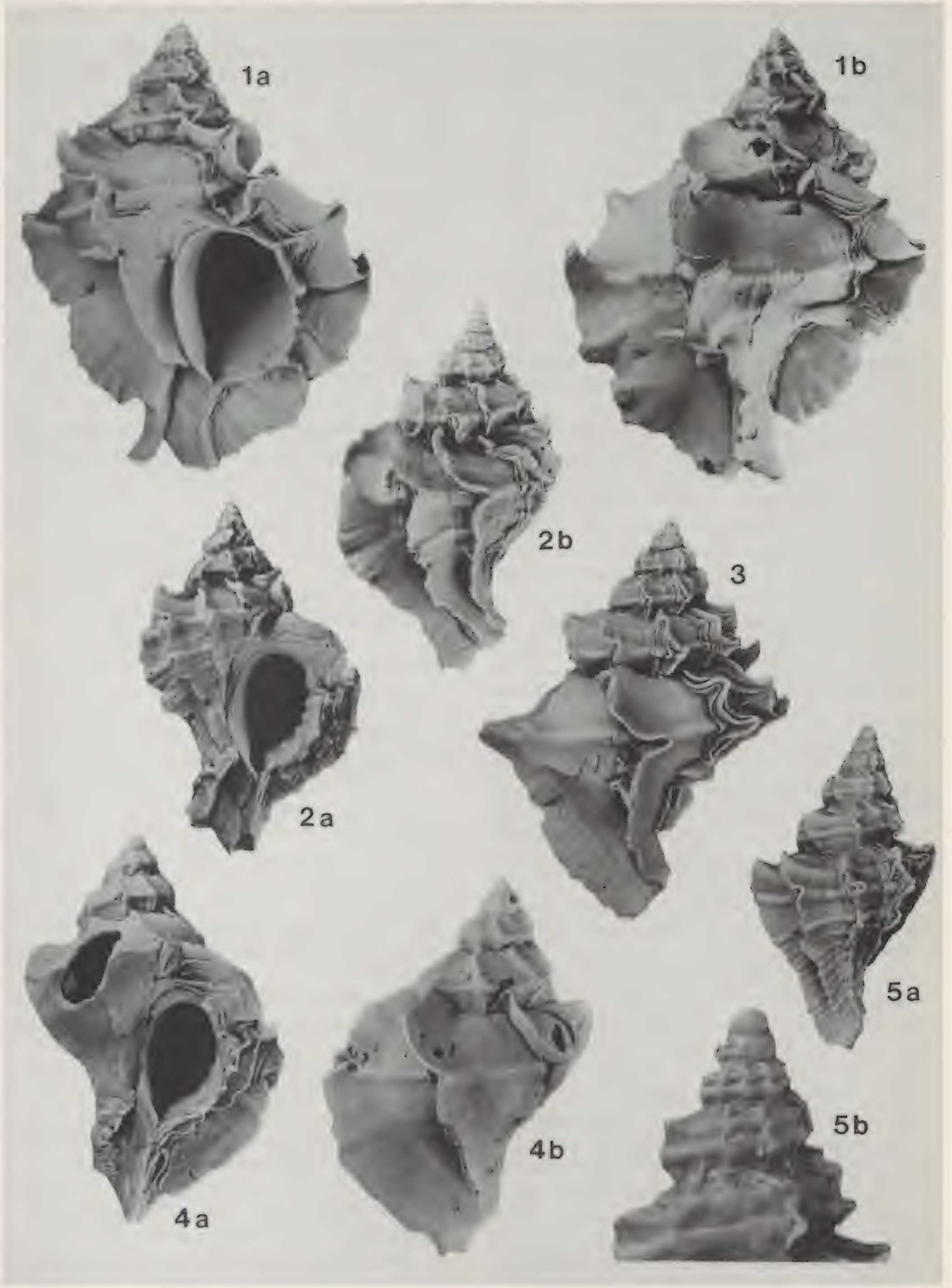


PLATE 5

Because *Pterorytis* was originally described as having six varices, Olsson and Harbison (1953, p. 252) erected the subgenus *Neurarhytis* for those species having only four varices on the last whorl. *Pterorytis umbrifer* is much more variable than Olsson and Harbison realized. We have material with from four (pl. 6, fig. 1) to nine varices (pl. 5, fig. 2) on the last whorl. In general, juvenile shells have more varices, mature shells have four or five varices on the body whorl.

Pterorytis shares with *Ceratostoma* the presence of a labral tooth near the base of the outer lip, situated at the end of a distinct external groove or fold. The genera differ in sculpture, however. The early whorls of *Ceratostoma* are cancellate, whereas those of *Pterorytis* bear about ten lamellar varices. On later whorls, *Ceratostoma* possesses three to four varices, between which is an intervarical node. In *Pterorytis* s.s., four to nine varices per whorl are connected by a strong peripheral keel, and there are no intervarical nodes or ribs. The subgenus *Microrhytis* is intermediate between the two, with three varices and strong intervarical nodes on each whorl, similar to *Ceratostoma,* but with lamellar varices on the early whorls, as in *Pterorytis*. It is our belief that the resemblance between the trivaricate *Microrhytis* line and *Ceratostoma* is the result of convergence.

There may be a close relationship between *Pterorytis* and *Ocinebrellus*. Indeed, Vokes (1988) described *Pterorytis* as an *Ocinebrellus* with a labral tooth. Typical species of *Ocinebrellus,* such as *O. inornatum* (Recluz, 1851) and *O. aduncus* (Sowerby, 1834), both living on temperate Pacific coasts of Asia, occasionally possess a small labral tooth formed just below the basal-most of four principal spiral cords. These cords are elaborated as points on the varices, which vary in number from three to seven, and which are unusual among muricids in being adaperturally reflected. The presence of three rather than four cords, and the abapertural instead of adapertural reflection of varices, distinguish *Pterorytis* from *Ocinebrellus*.

Although the genus *Pterorytis* does not persist in the western Atlantic past the end of the Pliocene (see Lyons, 1991, p. 146-150, for arguments for the Late Pliocene age of the formations in which the last *Pterorytis* specimens occur), the group is still living in the eastern Pacific with the species *P. hamatus* (Hinds, 1844). Emerson (1985) has illustrated a magnificent Ecuadorian specimen, having an ocenebrine radula and operculum, very like *P. umbrifer*, but with a denticulate outer lip, as in form *P. seminola*.

Radwin and D'Attilio (1976, p. 121, pl. 14, fig. 2) have figured as *"?Ocenebra hamata"* another very large specimen (66.8 mm) that seems to represent a different species, as Emerson suggested (1985, p. 16). Their shell cannot be assigned to any known species and may well prove to be a second species of *Pterorytis*, occurring off the coast of Peru.

Subgenus PTERORYTIS s.s.

PTERORYTIS (PTERORYTIS) UMBRIFER (Conrad)

Plate 5, figures 1-5; Plate 6, figures 1-5; Plate 7, figures 1-7; Text-figure 1

Murex umbrifer CONRAD, 1832, Fossil Shells Tert. Formations North America, v. 1, no. 1, p. 17, pl. 3, fig. 1 [reprinted by Harris, 1893, p. 31].

Not *Cerostoma umbrifer* (Conrad). TUOMEY and HOLMES, 1856, Pleiocene Fossils South Carolina, p. 141, pl. 28, fig. 14 [= *P. fluviana* Dall].

Not *Murex umbrifer* Conrad. EMMONS, 1858, Rept. North Carolina Geol. Survey, p. 247, fig. 104a [= *P. fluviana* Dall].

Murex (Pterorytis) umbrifer Conrad. CONRAD, 1863, Acad. Nat. Sci. Philadelphia, Proc., v. 14, p. 560.

Murex (Pterorhytis) umbrifer Conrad. CONRAD, 1868, Amer. Jour. Conch., v. 4, p. 64, pl. 5, fig. 7.

Ocenebra (Pterorhytis) umbrifer (Conrad). COSSMANN, 1903, Essais Paléoconch. Comp., v. 5, p. 43.

Purpura marshalli MANSFIELD, 1930, Florida State Geol. Survey, Bull. 3, p. 84, pl. 11, fig. 4.

Pterorhytis (Pterorhytis) umbrifer (Conrad). OLSSON and HARBISON, 1953, Acad. Nat. Sci. Philadelphia, Mon. 8, p. 252, pl. 35, fig. 2 ("paratype").

Pterorytis (Pterorytis) umbrifer (Conrad). EMERSON, 1959, Amer. Mus. Novitates, no. 1974, p. 3, fig. 1 ("paratypes").

Pterorytis (Neurarhytis) marshalli (Mansfield). EMERSON, 1959, Amer. Mus. Novitates, no. 1974, p. 5.

Pterorhytis umbrifer (Conrad). HALL, 1959, Jour. Paleontology, v. 33, no. 3, p. 432, pl. 63, fig. 6 (after Olsson and Harbison, 1953); PETUCH, 1994, Atlas Florida Foss. Shells, p. 9, pl. 44, fig. A.

Pterorhytis seminola OLSSON and PETIT, 1964, Bulls. Amer. Paleontology, v. 47, no. 217, p. 550, pl. 81, fig. 4; PETUCH, 1994, Atlas Florida Foss. Shells, pl. 44, fig. I only [fig. G = depauperate *P. fluviana* Dall].

Not *Pterorhytis (Neurarhytis) marshalli* (Mansfield). OLSSON and PETIT, 1964, Bulls. Amer. Paleontology, v. 47, no. 217, p. 549, pl. 81, figs. 3, 3a [= *P. fluviana* Dall].

[Pterorytis] umbrifer (Conrad). VOKES, 1971, Bulls. Amer. Paleontology, v. 61, no. 268, p. 113.

[Pterorytis] marshalli (Mansfield]. VOKES, 1971, Bulls. Amer. Paleontology, v. 61, no. 268, p. 123.

[Pterorytis] seminola Olsson and Petit. VOKES, 1971, Bulls. Amer. Paleontology, v. 61, no. 268, p. 126.

Not *Pterorytis umbrifer* (Conrad). CAMPBELL, 1974, South Carolina Geol. Notes, v. 18, no. 4, p. 79; CAMPBELL, CAMPBELL, and CARTER, 1995, Tulane Stud. Geol. Paleont., v. 27, nos. 1-4, p. 175 [= smooth form of *P. fluviana* Dall].

Pterorhytis umbrifer (Conrad). WARD and BLACKWELDER, 1980, U.S. Geol. Survey, Bull. 1482-D, p. D28.

Pterorytis umbrifer (Conrad). WARD and BLACKWELDER, 1980, U.S. Geol. Survey, Bull. 1482-D, p. D48; EMERSON, 1985, Nautilus, v. 99, no. 1, p. 16; CAMPBELL, 1993, Virginia Div. Nat. Res., Publ. 127, p. 76, pl. 33, fig. 367; WARD and GILINSKY, 1993, Virginia Mus. Nat. Hist., Mem. 3A, p. 18, table 5.

Not *Neurarhytis marshalli* (Mansfield). PETUCH, 1988, Neogene Hist. Trop. Amer. Moll., pl. 19, fig. 9 [= *P. fluviana* Dall].

Pterorhytis marshalli (Mansfield). PETUCH, 1994, Atlas Florida Foss. Shells, pl. 44, fig. C.

Description: "Fusiform, with 6 foliated reflected laminae; whorls angular and carinated; aperture obovate; beak recurved." (Conrad, 1832)

"Fusiform, with four [five!] very prominent, lamelliform ribs on the body whorl; whorls 6, angular, with a prominent revolving rib on the angle; two small ribs, the lowest one obsolete, on the body whorl, distant from the upper one; aperture ovate, surrounded by a raised margin, with a prominent, erect tooth near the base of the labrum; canal closed." (Conrad, 1868)

Shell with seven teleoconch whorls, protoconch of one and one-half rounded whorls. Shell surface completely smooth; of two layers: an outer translucent, easily decorticated calcitic layer; and a creamy, opaque aragonitic layer lining aperture. Axial ornamentation on first three teleoconch whorls of about ten lamellar flanges, reducing to nine on next two whorls, and then to seven by sixth teleoconch whorl. Usually four or five varices on seventh whorl; varices beginning as simple lamellae, gradually becoming more complex with multiple shell layers on adapertural face. Spiral ornamentation on earliest teleoconch whorls of two cords, that at periphery increasing in strength as that on shoulder ramp gradually weakens. On body whorl a third small cord sometimes developed anterior to major cord at periphery, and occasionally two additional smaller threads anterior to that. At intersection of spiral cords and axial lamellae abaperturally-directed folds developed, including on shoulder ramp, where the cord itself may no longer be apparent. In mature adult usually three major abaperturally-directed folds on each varix, sometimes forming hook-like extensions, largest at peripheral cord, smaller at secondary cords. Aperture oval, inner lip narrow and smooth, appressed only at posteriormost portion. Inner edge of outer lip extended well in advance of apertural varix; outer lip crenulated in harmony with spiral cords, smooth on most examples but some specimens with six elongate denticles on inner side of outer lip (especially in form *seminola*). On anterior portion of outer lip a strong tooth formed as a projection of outer varical lamella, coated by enamel of inner lip. Siphonal canal sealed over by a plate extending from columella wall to meet varical side; slightly recurved distally, causing former canals to diverge as spurs.

Lectotype: ANSP 79605; height 48.3 mm, diameter 32.5 mm (here designated).

Type locality: James River [Day's Point], Yorktown, Virginia.

Occurrence: Eastover Formation (Cobham Bay Member), Virginia; Yorktown Formation, Virginia and North Carolina; Raysor Formation and Goose Creek Limestone, South Carolina;

Jackson Bluff Formation and lower Pinecrest beds, Florida.

Figured specimens: PLATE 5: Fig. 1, USNM 488713; height 52.1 mm, diameter 42.0 mm; locality TU 613. Fig. 2, USNM 488714; height 33.5 mm, diameter 20.5 mm; locality, Chuckatuck, Virginia (Blow Coll.). Fig. 3, USNM 488715; height 37.8 mm, diameter 30.0 mm; locality, Day's Point, James River, Virginia (Blow Coll.). Fig. 4, USNM 488716; height 36.0 mm, diameter 25.4 mm; locality, Yadkin, City of Chesapeake, Virginia (Campbell Coll.). Fig. 5, USNM 488717; height 10.9 mm, diameter 6.0 mm; locality, Rock Wharf, Smithfield, Virginia (Campbell Coll.). PLATE 6: Fig. 1, USNM 488718; height 45.0 mm, diameter 30.0 mm; locality TU 60. Fig. 2, USNM 488719; height 12.5 mm, diameter 7.5 mm; locality TU 60. Fig. 3, USNM 488720; height 42.2 mm, diameter 30.5 mm; locality TU 60. Fig. 4, Stephens Collection; height 49.0 mm, diameter 33.6 mm; locality TU 1524. Fig. 5, Stephens Collection; height 57.9 mm, diameter 41.2 mm; locality TU 1512. PLATE 7: Fig. 1, USNM 488721; height 38.8 mm, diameter 26.7 mm; locality TU 730. Fig. 2, USNM 488722; height 27.9 mm, diameter 18.2 mm; locality TU 730. Fig. 3, USNM 488723; height 37.0 mm, diameter 23.7 mm; locality TU 932. Fig. 4, USNM 488724; height 32.6 mm, diameter 19.6 mm; locality TU 729. Fig. 5, USNM 488725; height 32.7 mm, diameter 25.0 mm; locality TU 729. Fig. 6, USNM 488726; height 30.8 mm, diameter 23.1 mm; locality TU 729. Fig. 7, USNM 488727; height 19.2 mm, diameter 12.7 mm; locality TU 729. Other occurrences: TU localities 534, 728, 789, 796, 797, 842, 855, 980, 1044.

Discussion: In the collections of the Academy of Natural Sciences, Philadelphia, there are three specimens indicated as "syntypes" of *Murex umbrifer* Conrad. The best of these (ANSP 13787; height 50.8 mm) is the one figured by Olsson and Harbison (1953, pl. 35, fig. 2) as a "paratype" and later figured by Emerson (1959, fig. 1) as "paratypes" (although his three views are all of the same specimen). But there is no evidence that there is either a holotype or a lectotype (Conrad's work predates such taxonomic constraints) and, thus, this specimen is properly a syntype (ICZN Code, Art. 73b). All things being equal, this specimen perhaps should be designated as the lectotype. However, there is a second specimen (ANSP 79605; height 48.3 mm), which is clearly the one illustrated by Conrad in 1868 (see text-fig. 1). Therefore, this second specimen is here designated as the lectotype and specimen no. ANSP 13787 becomes a paralectotype*. There is also a third, smaller specimen (ANSP 13787; height 20.8 mm), which becomes a second paralectotype.

Originally *P. umbrifer* was named from the Yorktown Formation, Virginia, and no one seems to have been willing to admit the possiblity that it might also occur as far south as Florida. (Now, of course, we recognize numerous species in common between the Yorktown, Jackson Bluff, and Pinecrest units). When Mansfield described *P. marshalli*, he compared it with *P. fluviana* Dall, noting that *P. marshalli* has "more erect and thinner varices" than *P. fluviana*, which is true; but they

*Moore's citation of ANSP 13841 as "possible syntype" for *Murex umbrifer* (1962, Proc. Acad. Nat. Sci. Philadelphia, v. 114, no. 2, p. 106) is an error. That number refers to a specimen of *Fasciolaria (Triplofusus) scalarina* Heilprin figured by Olsson and Harbison (1953, pl. 35, fig. 1a).

PLATE 6

Figures Page

1-5. *Pterorytis (Pterorytis) umbrifer* (Conrad) 90

1. (X 1 1/4) USNM 488718; height 45.0 mm, diameter 30.0 mm.
   Locality: TU 60; Jackson Bluff Formation.
2. (X 4) USNM 488719; height 12.5 mm, diameter 7.5 mm.
   Locality: TU 60; Jackson Bluff Formation.
3. (X 1 1/4) USNM 488720; height 42.2 mm, diameter 30.5 mm.
   Locality: TU 60; Jackson Bluff Formation.
4. (X 1 1/4) Stephens Collection; height 49.0 mm, diameter 33.6 mm.
   Locality: TU 1524; Pinecrest beds.
5. (X 1) Stephens Collection; height 57.9 mm, diameter 41.2 mm.
   Locality: TU 1512; Pinecrest beds.

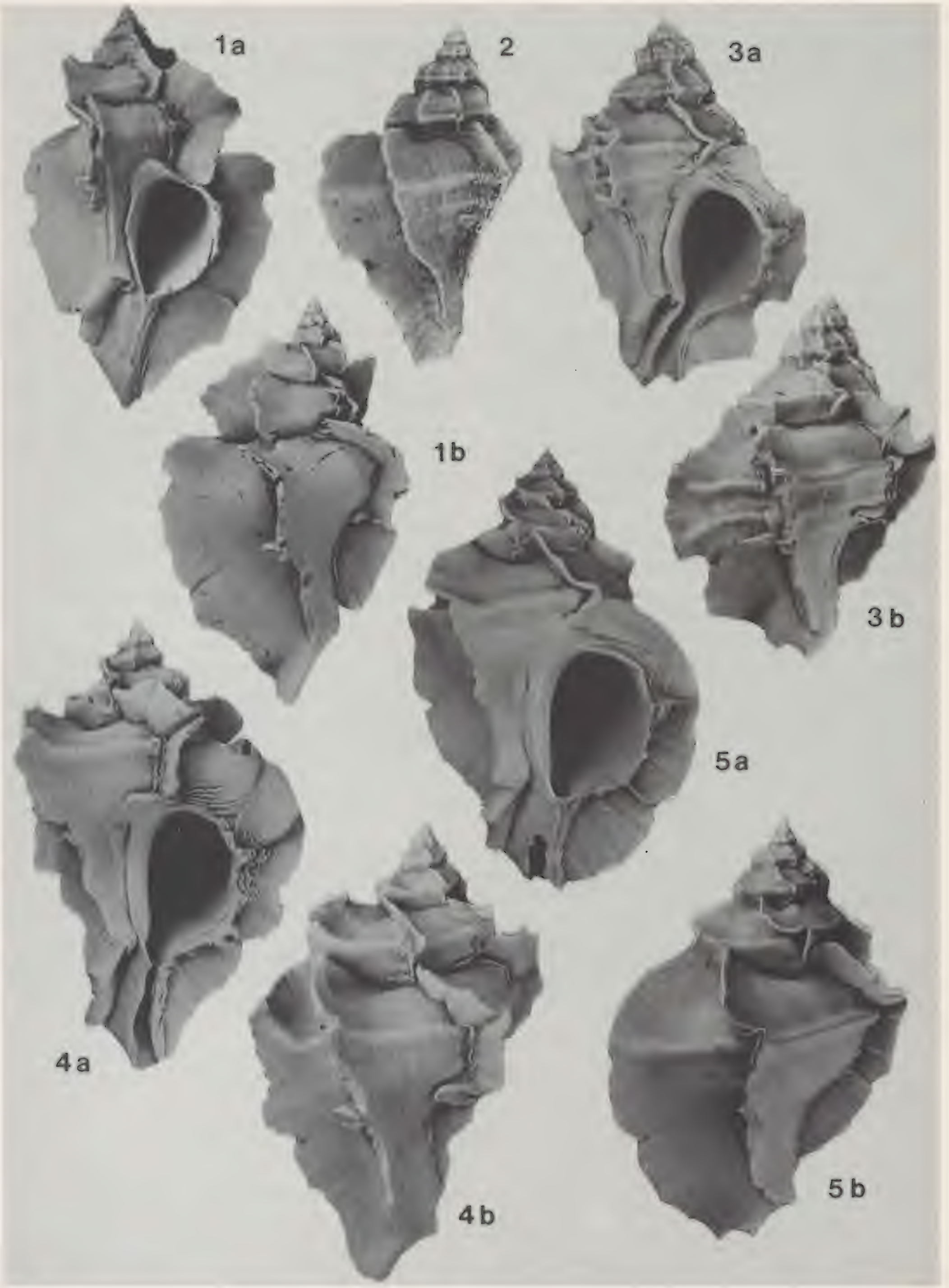


PLATE 6

are identical to those in *P. umbrifer*.

There seems to be a slight stratigraphic difference between the two species of *Pterorytis*. According to Ward and Blackwelder (1980, p. D28) *Pterorytis umbrifer* first appears in the latest Miocene Cobham Bay Member of the Eastover Formation and material provided by L.W. Ward confirms the identification. Based on our collections, *P. umbrifer* occurs in the Pliocene beds of the Yorktown Formation, Jackson Bluff, and lower Pinecrest beds. In South Carolina it also occurs in the Raysor Formation and the lower Goose Creek Limestone (L.D. Campbell, pers. comm.). Although *P. fluviana* first appears together with *P. umbrifer* in the Pinecrest beds in southern Florida, it really begins to flourish only with the disappearance of *P. umbrifer* and is found in the lower Caloosahatchee and Nashua formations in Florida, the correlative lower Waccamaw and Cypresshead formations in South Carolina, and at Aurora, North Carolina (TU 1022), in beds that Ward and Blackwelder (1987, p. 116) assign to the Early Pleistocene James City Formation but which Lyons (1991, p. 148) convincingly argues are more likely to be of Late Pliocene (lower Caloosahatchee Formation equivalent) age.

Along the Kissimmee River between Ft. Basinger and the north side of Lake Okeechobee there is a most enlightening sequence of occurrence of the two species, which documents the above statement. Table 1 shows the replacement of *P. umbrifer* by *P. fluviana*.

Pterorytis umbrifer is extremely variable, as we have attempted to demonstrate in pls. 5-7. L. Campbell (1993, p. 76) has given a good discussion of the various forms, noting that there are three distinct varical patterns, almost certainly environmentally controlled. These are: (1) "varices low, thick, and massive (*P. seminola* Olsson and Petit, 1964), apparently reflective of high energy conditions" [see pl. 5, fig. 4; pl. 7, figs. 3, 4]; (2) the typical form with "thin, erect blades with fluting at intersection of spiral cords, and frilled lamellae on apertural side of varix," coming from quiet water habitats [see pl. 5, figs. 1, 2]; and (3) with "very thin, erect, recurved blades with strongly recurved open spines at intersection of spiral cords, a form apparently from sheltered habitats" [see pl. 5, fig. 3].

In southern Florida there is yet another form, which we will call "form no. 4," with thin, erect *unfluted* varices, lacking the typical shoulder carina. Although we have a single example from Jackson Bluff (TU 60; pl. 6, fig. 1), it is common in a restricted area along the Kissimmee River (TU 729; pl. 7, figs. 5, 6), where it occurs together with the *"seminola"* morphotype, and seems to represent the "last gasp" of the species in the geologic record. In addition to the loss of the shoulder carina, the shells often have either a greatly reduced labral tooth, or none at all, suggesting that the loss of the labral tooth seen in *P. roxaneae* (below) is an orthogenetic trait. However, it should be noted that "toothless" examples can occur anywhere in the section, such as at TU 730, one of the oldest occurrences (pl. 7, fig. 2).

Not only does the number and nature of the varices display great variation, but also the absence or presence of denticles on the inner side of the outer lip. The heavy, short-varixed form named *P. seminola* always has these denticles, but they also appear sporadically in the typical *P. umbrifer* form (pl. 5, fig. 2), as well as in the holotype of *P. marshalli* (see Mansfield, 1930, pl. 11, fig. 4).

PTERORYTIS (PTERORYTIS) FLUVIANA Dall
Plate 8, figures 1-7; Plate 9, figures 1-5;
Plate 10, figures 1-8; Text-figures 2, 3

Cerostoma umbrifer (Conrad). TUOMEY and HOLMES, 1856, Pleiocene Foss. South Carolina, p. 141 (in part), pl. 28, fig. 14 (*not* of Conrad).

Murex umbrifer Conrad. EMMONS, 1858, Rept. North Carolina Geol. Survey, p. 247, fig. 104a (*not* of Conrad).

Murex (Pterorhytis) conradi DALL, 1890, Wagner Free Inst. Sci., Trans., v. 3, pt. 1, p. 143, pl. 12, figs. 8, 11 [as *Pterorhytis conradi*] (for *Cerostoma umbrifer* Tuomey and Holmes, 1856, *not* of Conrad). Not *Murex conradi* d"Orbigny, 1850, unnecessary *n.n. pro Murex mantelli* Conrad.

Pterorhytis (Conradiana Dall var.?) *fluviana* DALL, 1903, Wagner Free Inst. Sci., Trans., v. 3, pt. 6, p. 1633 [pl. expl.], pl. 60, figs. 20,

21 [not in text].

Ocenebra (Pterorhytis) Conradi (Dall). COSSMANN, 1903, Essais Paléoconch. Comp., v. 5, p. 43, text-fig. 2 [incorrectly labeled fig. 3].

Murex (Pterorhytis) conradi Dall. MARTIN, 1904, Maryland Geol. Survey, Miocene, p. 200, pl. 50, figs. 9, 9a (after Dall, 1890).

Purpura fluviana (Dall). MANSFIELD, 1930, Florida State Geol. Survey, Bull. 3, p. 83, pl. 11, fig. 7 (holotype).

Pterorhytis (Neurarhytis) fluviana (Dall). OLSSON and HARBISON, 1953, Acad. Nat. Sci. Philadelphia, Mon. 8, p. 253, pl. 35, fig. 3.

Pterorytis (Neurarhytis) fluviana (Dall). EMERSON, 1959, Amer. Mus. Novitates, no. 1974, p. 4, fig. 2 (after Dall, 1903); EMERSON, 1985, Nautilus, v. 99, no. 1, p. 16.

Pterorytis (Neurarhytis) conradi (Dall). EMERSON, 1959, Amer. Mus. Novitates, no. 1974, p. 5, fig. 3 (after Dall, 1890).

Pterorhytis (Neurarhytis) marshalli (Mansfield). OLSSON and PETIT, 1964, Bulls. Amer. Paleontology, v. 47, no. 217, pl. 81, figs. 3, 3a (*not* of Mansfield).

[Pterorytis] conradi (Dall). VOKES, 1971, Bulls. Amer. Paleontology, v. 61, no. 268, p. 34.

[Pterorytis] conradiana Dall. VOKES, 1971, Bulls. Amer. Paleontology, v. 61, no. 268, p. 120.

[Pterorytis] fluviana Dall. VOKES, 1971, Bulls. Amer. Paleontology, v. 61, no. 268, p. 121.

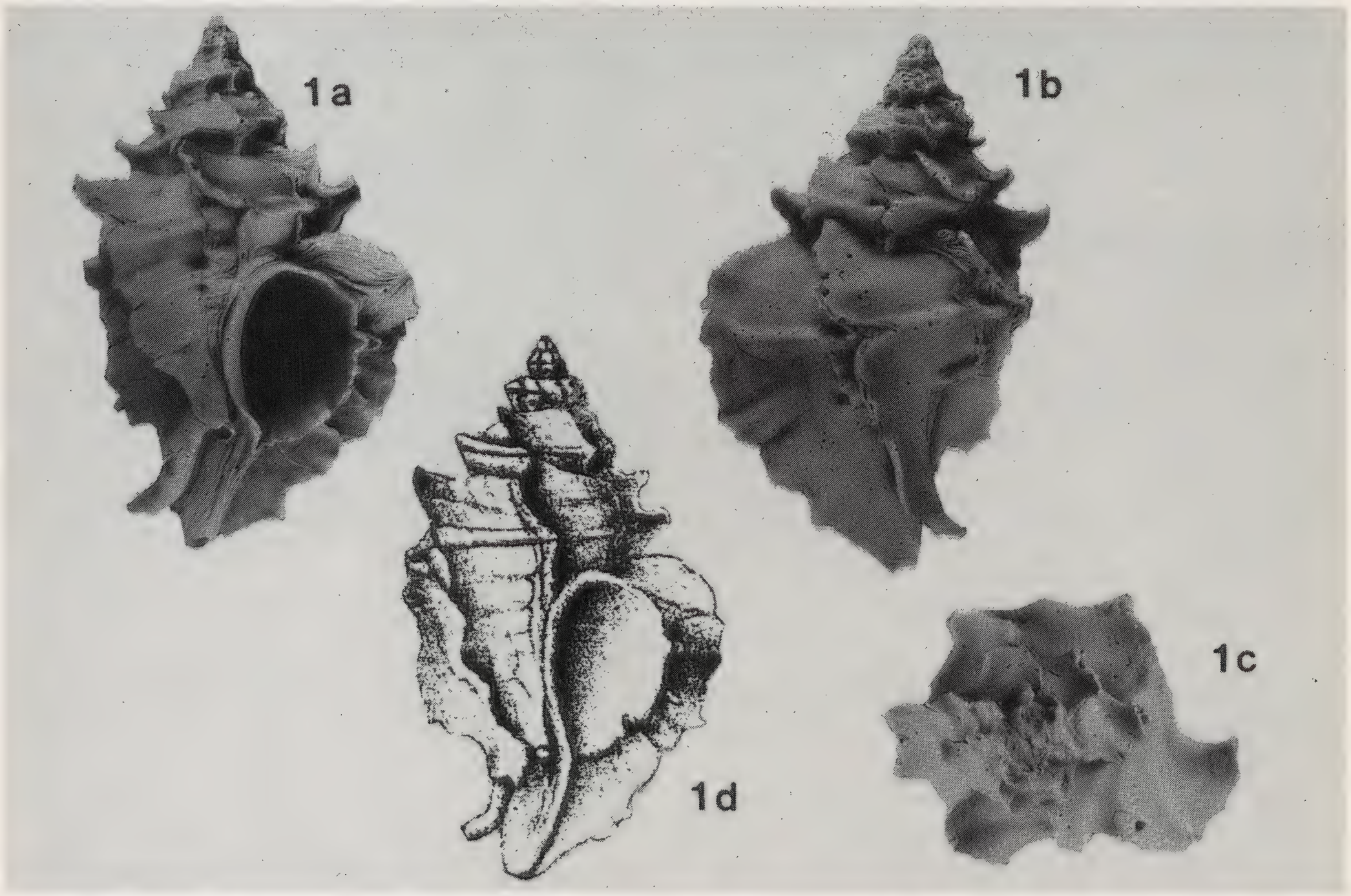
Pterorytis conradi (Dall). CAMPBELL, 1974, South Carolina Geol. Notes, v. 18, no. 4, p. 79; WARD and GILINSKY, 1993, Virginia Mus. Nat. Hist., Mem. 3A, p. 18, table 5.

Pterorytis umbrifer (Conrad). CAMPBELL, 1974, South Carolina Geol. Notes, v. 18, no. 4, p. 79; CAMPBELL, CAMPBELL, and CARTER, 1995, Tulane Stud. Geol. Paleont., v. 27, nos. 1-4, p. 175 (*not* of Conrad).

Pterorhytis conradi (Dall). WARD and BLACKWELDER, 1987, Smithsonian Cont. Paleobiol., no. 61, p. 174, pl. 39, figs. 7, 8; LYONS, 1991, Florida Mus. Nat. Hist., Bull. (Biol. Sci.), v. 35, no. 3, p. 148.

Pterorhytis fluviana (Dall). PETUCH, 1988, Neogene Hist. Trop. Amer. Moll., p. 51, pl. 13, fig. 5; PETUCH, 1994, Atlas Florida Foss. Shells, pl. 44, fig. B.

Neurarhytis marshalli (Mansfield). PETUCH, 1988, Neogene Hist. Trop. Amer. Moll., pl. 19,



Text-figure 1. *Pterorytis (Pterorytis) umbrifer* (Conrad). A-C, ANSP 79605 (lectotype; here designated); height 48.3 mm, diameter 32.5 mm; locality, James River, Virginia. D, Conrad, 1868, pl. 5, fig. 7. (X 1)

fig. 9 (*not* of Mansfield).

Pterorhytis lindae PETUCH, 1994, Atlas Florida Foss. Shells, p. 282, pl. 44, figs. J, K.

Pterorhytis squamulosa PETUCH, 1994, Atlas Florida Foss. Shells, p. 283, pl. 44, figs. D, E.

Pterorhytis wilsoni PETUCH, 1994, Atlas Florida Foss. Shells, p. 284, pl. 44, fig. F.

Pterorhytis seminola Olsson and Petit. PETUCH, 1994, Atlas Florida Foss. Shells, pl. 44, fig. G only (*not* of Olsson and Petit).

Description: "This fine species has, like most of the species of this genus, only four varices. The spire is much shorter than in *M. umbrifer* and the form of the varices is different." (*Murex conradi* Dall, 1890)

"Shell of moderate size, solid, with about 1 1/2 corroded nuclear and 4 strong angulated postnuclear whorls. Whorls rapidly enlarging; body whorl about three-fourths the shell length. Suture deep, not appressed. Axial sculpture of 4 reflected, rather thin, facially undulated, marginally sinuate varices on the later whorls and of about 9 ribs on the early whorls. Face of varices with thin marginally crenulated laminae which are very faint between the varices. Spiral sculpture of about 3 faint, rounded lines situated at and below the periphery. Aperture broadly ovate; outer lip with a small denticle situated at anterior part. Canal closed, moderately twisted." (*P. fluviana* Dall – Mansfield, 1930)

Holotype: USNM 163801; height 35.1 mm, diameter 24.7 mm.

Type locality: Caloosahatchee Formation; USGS 3300, Shell Creek, Charlotte County, Florida (= TU 539B).

Occurrence: Pinecrest beds (upper beds only), lower Caloosahatchee and Nashua formations, Florida; Waccamaw and Cypresshead formations, South Carolina; Waccamaw, Duplin and "James City" (of Ward and Blackwelder, 1987) formations, North Carolina.

Figured specimens: PLATE 8: Fig. 1, USNM 114122; height 22.5 mm, diameter 14.0 mm; locality USGS 2280, Natural Well, North Carolina (= TU 376). Fig. 2, USNM 488728; height 32.0 mm, diameter 20.8 mm; locality TU 1022. Fig. 3, Stephens Collection; height 45.0 mm, diameter 25.0 mm; locality TU 1022. Fig. 4, USNM 488729; height 24.0 mm, diameter 15.2 mm; locality TU 558. Fig. 5, USNM 488730; height 25.5 mm, diameter 18.2 mm; locality, Calabash, North Carolina (Campbell Coll.). Fig. 6, USNM 488731; height 32.4 mm, diameter 19.6 mm; locality TU 870. Fig. 7, UF 20435; height 12.5 mm, diameter 6.0 mm; locality TU 558. PLATE 9: Fig. 1, Stephens Collection; height 37.4 mm, diameter 25.0 mm; locality TU 1512. Fig. 2, Stephens Collection; height 36.0 mm, diameter 21.2 mm; locality TU 1512. Fig. 3, Stephens Collection; height 12.8 mm, diameter 9.0 mm; locality TU 1512. Fig. 4, USNM 488732; height 32.1 mm, diameter 22.1 mm; locality TU 768. Fig. 5, Stephens Collection; height 45.5 mm, diameter 33.2 mm; locality TU 1000. PLATE 10: Fig. 1, USNM 488733; height 35.4 mm, diameter 24.7 mm; locality TU 728. Fig. 2, USNM 488734; height 36.9 mm, diameter 22.1 mm; locality TU 729. Fig. 3, USNM 488735; height 32.4 mm, diameter 22.5 mm; locality TU 729. Fig. 4, USNM 488736; height 37.2 mm, diameter 21.0 mm; locality TU 729. Fig. 5, USNM 488737; height 32.5 mm, diameter 19.2 mm; locality TU 729. Fig. 6, Stephens Collection; height 39.4 mm, diameter 25.7 mm; locality TU 1000. Fig. 7, USNM 488738; height 42.8 mm, diameter 27.7 mm; locality TU 729. Fig. 8, Stephens

North <----------> South
Pinecrest <----------> Caloosahatchee

TU locality	730	932	728	729	769	770
P. umbrifer	28	30	0	0	0	0
f. *"seminola"*	5	3	1	21	0	0
f. "no. 4"	0	0	0	27	0	0
P. fluviana	9	39	12	155	2	31
f. *"lindae"*	0	0	0	8	0	5
f. *"squamulosa"*	0	0	0	2	1	0

Table 1. Distribution of species of *Pterorytis* along Kissimmee River, Okeechobee County, Florida. For descriptions of the various "forms" see text.

Collection; height 31.9 mm, diameter 19.8 mm; locality TU 729. Other occurrences: TU locality nos. 68, 376, 520, 523, 539B, 559, 726, 759, 767, 769, 770, 1493.

Discussion: The nomenclature of this species is more complicated than most. Originally, Tuomey and Holmes (1856, pl. 28, fig. 14) illustrated a shell, which they identified as *Cerostoma umbrifer* (Conrad), stating that it came from "Smith's, Goose Creek." Dall (1890, p. 143) pointed out that their specimen was not the same as Conrad's *umbrifer* and so named it *Murex conradi*, repeating the Goose Creek locality and adding to it, "St. Mary's River, Maryland."

Unfortunately, the name *Murex conradi* had already been used by d'Orbigny in his *Prodrome de Paléontologie* (1850, p. 364) as an unnecessary new name for *Murex mantelli* Conrad, 1833. This work of d'Orbigny is a paleontologic nomenclator, in which the author renamed a vast number of preoccupied and misidentifed species. In the majority of the cases, the new names are justified and have come into the literature as the correct name for the species in question. In the case of *Murex conradi* there is no known reason for such a replacement name; nevertheless it was validly proposed and, therefore, must preoccupy *Murex conradi* Dall.

Whether Dall became aware of the d'Orbigny work, or whether it was a simple lapsus, in 1903 Dall named a second taxon, "*Pterorhytis (Conradiana* var.?*) fluviana.*" The name is not mentioned in the text, but only in the plate explanation, and this is the only reference to a change of name for *Murex conradi* Dall. Boss, Rosewater, and Ruhoff (1968, p. 88) take the position that this is an emendation for *M. conradi*, but we really have no way of knowing.

To further complicate the matter, *P. fluviana* is just a less fimbriate variety of *M. conradi*, as Dall suggested (compare textfigures 2, 3). Thus, we have three possible names for this species: *P. conradi, P. conradiana,* and *P. fluviana*. Given the ambiguous nature of the proposals for both *Murex conradi* d'Orbigny and *Pterorhytis conradiana* Dall, it seems in the best interest of nomenclatorial stability to accept *P. fluviana* Dall as the valid name.

A major factor in choosing *P. fluviana* as the correct name is the fact that not only is the taxonomy of *Murex conradi* confused but the locality information is as well. The species does not occur in the Goose Creek fauna (see Campbell and Campbell, 1995, p. 99) or the St. Mary's River fauna. Ward and Blackwelder (1987, p. 174) discussed the problems involved, concluded the locality data had been switched, and recommended that Wilmington, North Carolina, be designated as the type locality. If one accepts that in 1890 "Wilmington" could have included an area stretching some 40 miles to the west and south, this is as good a solution as possible. The type specimen has the scabrous surface typical of the elaborately ornamented form that occurs in the lower Waccamaw Formation, at such places as Calabash, North Carolina (see pl. 8, fig. 5), and it is probable that the type specimen actually came from the Waccamaw River. In the Tulane Collections we have specimens identical to the type from near Myrtle Beach, South Carolina (TU 558; pl. 8, fig. 4).

There is also a problem with the reference to the Goose Creek fauna. As noted above, the species does not occur in the Goose Creek Limestone; however, Campbell and Campbell (1995, p. 63) have indicated that the Tuomey and Holmes species said to be from "Smith's, Goose Creek" are a mixture of both the moldic Goose Creek Limestone and a well-preserved molluscan fanule of lower Waccamaw-aged material, which they assign to the lower Cypresshead Formation. Thus, there is no reason that the "Goose Creek" locality of Tuomey and Holmes should be replaced, only the idea that it came from the Goose Creek Limestone.

Although Schuchert *et al.* (1905, p. 420) list "cotypes" for *Murex (Pterorhytis) conradi* from St. Mary's River, Maryland, the original catalogue indicates a single specimen (USNM 87749), which is that one figured by Dall (1890, pl. 12, figs. 8, 11). This may just be a mistake or, perhaps, they were including the Tuomey and Holmes figured specimen as one of the "cotypes"; if

so, it is lost. According to Dr. W.K. Emerson (*in litt.*, 7/20/95) this specimen is not in the Tuomey and Holmes material at the American Museum of Natural History. Presumably the mislabeled "St. Mary's" specimen is the only one in the actual type lot and should be considered the holotype.

In the northern area this species replaces *P. umbrifer* in all of the beds above the Yorktown, including the Duplin Formation. Although P. umbrifer has been reported in the literature from the Duplin Formation (S. Campbell, 1974, p. 79; Campbell, Campbell, and Carter, 1995, p. 175) all of the material seen from Natural Well (TU 376, and USNM 114121, 114122) and Tearcoat Branch (Campbell Coll,) is referable to *P. fluviana* (pl. 8, fig. 1).

In Florida it occurs in all of the units from the Pinecrest (often occurring together with *P. umbrifer*, as noted above) through the lower Caloosahatchee Formation in the south and the Nashua Formation in northeastern Florida (specimen UF 74450, from locality PU004, Putnam County, in the collections of the Florida Museum of Natural History). We have a single specimen from locality TU 759, which otherwise seems to be "pure" Bermont, but with spoil-pile collecting one is never certain. At none of the other "unequivocal" Bermont localities do we have any specimens, and it seems probable that the one from locality TU 759 is actually from the Caloosahatchee Formation.

This lack of *P. fluviana* in the Early Pleistocene Bermont Formation tends to corroborate Lyons's (1991, p. 148) argument that the "James City Formation" of Ward and Blackwelder (1987) should be correlated with the Late Pliocene portion of the Caloosahatchee Formation. He (*ibid.*, p. 150) makes a very telling point when he states: "It is doubtful that the thermophilic taxa that characterized the Caloosahatchee fauna could have survived in the Carolinas an event [the onset of the Nebraskan Glacial Stage] that caused their extinction and replacement in south Florida."

The original differentiation between *P. conradi* and *P. fluviana* was primarily geographic, with *P. conradi* from the Carolinas and *P. fluviana* from Florida. But we have specimens from southern Florida that are as squamose as the type of *P. conradi*. As with *P. umbrifer*, this is an extremely variable species, ranging from the highly ornamented form named *P. conradi* (and *P. squamulosa* Petuch, 1994) (pl. 10, figs. 1-3, 6, 8) to relatively smooth shells named *P. fluviana* (and *P. wilsoni* Petuch, 1994) (pl. 9, figs. 1, 2, 5). Some examples along the Kissimmee River at locality TU 729 develop elaborately recurved varices and have been named *P. lindae* Petuch, 1994 (pl. 10, fig. 7). Perhaps the most ornate specimens of all are those that come from the Waccamaw Formation, to the southwest of Wilmington (pl. 8, figs. 4-6). But it is also possible to find examples so smooth as to be hard to distinguish from *P. umbrifer* (pl. 10, fig. 4), leading to Campbell's (1974, p. 79) and

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PLATE 7

Figures Page

1-7. *Pterorytis (Pterorytis) umbrifer* (Conrad) 90

1. (X 1 1/2) USNM 488721; height 38.8 mm, diameter 26.7 mm. Locality: TU 730; Pinecrest beds.
2. (X 1 1/2) USNM 488722; height 27.9 mm, diameter 18.2 mm. Locality: TU 730; Pinecrest beds.
3. (X 1 1/2) USNM 488723; height 37.0 mm, diameter 23.7 mm. Locality: TU 932; Pinecrest beds.
4. (X 1 1/2) USNM 488724; height 32.6 mm, diameter 19.6 mm. Locality: TU 729; Pinecrest beds.
5. (X 1 1/2) USNM 488725; height 32.7 mm, diameter 25.0 mm. Locality: TU 729; Pinecrest beds.
6. (X 1 1/2) USNM 488726; height 30.8 mm, diameter 23.1 mm. Locality: TU 729; Pinecrest beds.
7. (X 2 1/2; X 10) USNM 488727; height 19.2 mm, diameter 12.7 mm. Locality: TU 729; Pinecrest beds.

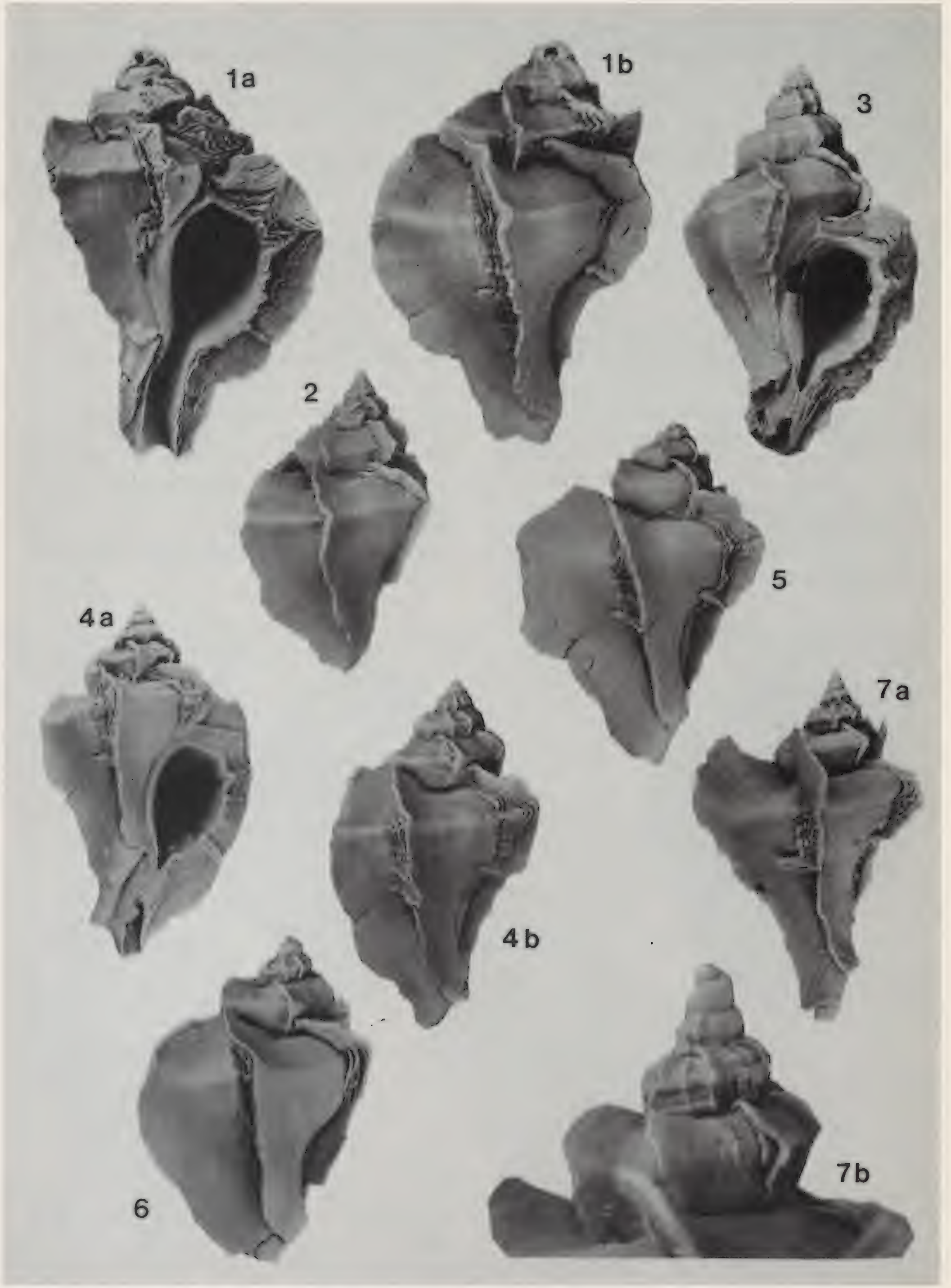


PLATE 7

Campbell, Campbell, and Carter's (1995, p. 175) citations of *P. umbrifer* from the Duplin Formation. Although rare, some specimens of *P. fluviana* exhibit labial denticles; such a specimen (presumably) was figured by Petuch (1994, pl. 44, fig. G) as *"P. seminola"* (pl. 10, fig. 5).

With so much variablity in both *P. umbrifer* and *P. fluviana*, one wonders where to draw the line between the two species. And the only absolute means of separation is the fact that in *P. umbrifer* the intervarical area is *always* completely smooth, even though there may be a fimbriate adapertural face to the varices. In *P. fluviana*, the intervarical area may be relatively smooth, but faint fimbriations are always present. In *P. umbrifer* the varices are thinner, and almost invariably there is a abapertural fold at the shoulder, even on those specimens where the shoulder cord is barely present. In *P. fluviana* the varices have no fold at the shoulder and they are more abaperturally recurved. In truth, given any one specimen it may be difficult deciding on the proper placement, but with a suite of specimens, the differentiation becomes easier.

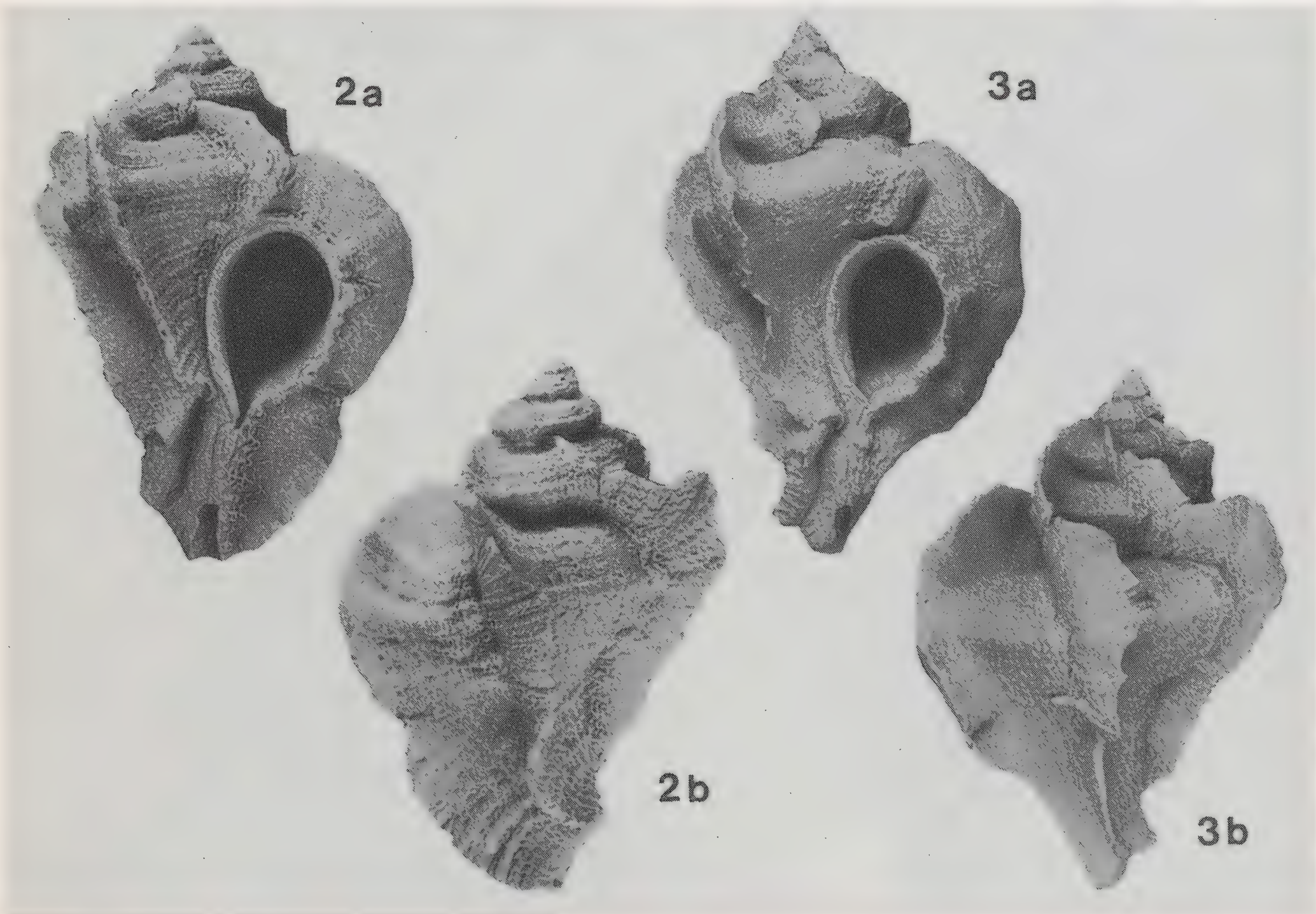
PTERORYTIS (PTERORYTIS) ROXANEAE Petuch
Plate 11, figures 1-4

Pterorhytis roxaneae PETUCH, 1994, Atlas Florida Foss. Shells, p. 283, pl. 44, fig. H.

Description: "Shell of average size for genus, thin, lightweight, inflated, with 4 thin, blade-like varices per whorl; shoulder angled but slightly rounded, without strong shoulder cord; intervarical areas smooth, waxy, without axial or spiral sculpture; wings smooth, without sculpture; aperture wide, open; lip edged with small crenulations; apertural tooth absent; siphonal canal proportionally short, without sculpture." (Petuch, 1994)

Holotype: UF 66254; height 33.3 mm, diameter 21.5 mm.

Type locality: Pinecrest beds (uppermost beds



Text-figure 2. *Pterorytis (Pterorytis) conradi* (Dall), USNM 87749 (holotype); height 35.2 mm, diameter 26.2 mm; locality "St. Mary's River, Md. (Clark)" [? = Wilmington, North Carolina]. Text-figure 3. *Pterorytis (Pterorytis) fluviana* Dall, USNM 163801 (holotype); height 35.1 mm, diameter 24.7 mm; locality USGS 3300, Shell Creek, Charlotte Co., Florida. (Both X 1 1/2)

only), from Petuch Unit 3, Phase 6 pit, Quality Aggregates, Inc., Sarasota, Sarasota County, Florida (= TU 1524).

Occurrence: Pinecrest beds (uppermost only), Florida.

Figured specimens: Fig. 1, Stephens Collection; height 34.2 mm, diameter 21.6 mm; locality TU 1524. Fig. 2, Stephens Collection; height 27.1 mm, diameter 18.4 mm; locality TU 1524. Fig. 3, Stephens Collection; height 26.1 mm, diameter 17.6 mm; locality TU 1524. Fig. 4, Stephens Collection; height 51.0 mm, diameter 36.0 mm; locality TU 1000.

Discussion: Petuch (1994, p. 283, pl. 44, fig. H) described *P. roxaneae* from his Unit 3 ("uppermost Pinecrest beds") in the Phase 6 Pit, Quality Aggregates, Inc., Sarasota, Florida (= TU 1524). These beds contain typical Caloosahatchee fossils, such as *Cypraea problematica* Heilprin, 1886, as well as endemics like the muricid *Hexaplex jameshoubricki* Petuch, 1994, and may be part of the so-called "*Trochita* beds" (Lyons, personal communication), of uppermost Pinecrest age.

Pterorytis roxaneae is unique in the absence of a labral tooth, and has a relatively thin shell. The varices are blade-like and slightly recurved, lacking a fold on the shoulder. In the original description, Petuch characterizes the varices as "wings smooth, unsculptured" and the intervarical surface as "smooth, waxy, without axial or spiral sculpture" (1994, p. 283). However, the varices are adorned by slightly abaperturally curved points, including one at the shoulder. The holotype of *P. roxaneae* is a worn shell, lacking the labral varix. Most specimens, however, have traces of fimbriation in the intervarical area (pl. 11, figs. 2, 3) and are distinctly fimbriate on the varical faces.

The relatively smooth intervarical areas in *P. roxaneae* resemble those of specimens of *P. fluviana* from the Caloosahatchee Formation in the area to the west of Lake Okeechobee, including St. Petersburg (TU 68; see Olsson and Harbison, 1953, pl. 35, fig. 3), Arcadia (TU 1512; pl. 9, figs. 1, 2), Shell Creek (TU 539B; see Dall, 1903, pl. 60, fig. 21), and the Caloosahatchee River (TU 768; see pl. 9, fig. 4). In the Stephens Collection there is one beautiful example of the smooth form of *P. fluviana* from the APAC pit at Sarasota (TU 1000; pl. 9, fig. 5), across the road from the type locality of *P. roxaneae*. We assume this specimen comes from the Caloosahatchee Formation portion of the section.

Subgenus MICRORHYTIS Emerson, 1959

Microrhytis EMERSON, 1959, Amer. Mus. Novitates, no. 1974, p. 6.

Type species: *Pterorytis (Microrhytis) pecki* Emerson, 1959, by original designation.

Description: "Shell purpuroid, small for the genus, with three low varices per whorl; ventral surface of each varix weakly sculptured with lace-like lamellae. Spinose apertural tooth retained by varices of the body whorl; apertural tooth small, anteriorly located on nodose inner lip." (Emerson, 1959)

Discussion: As discussed further in a study of the muricids of the Angostura Formation of Ecuador (Vokes, 1989b, p. 113), *Microrhytis* differs from the genus *Ceratostoma* in the nature of the early teleoconch whorls. In *Ceratostoma* there are no varices but the whorls are simply cancellate until approximately the fifth teleoconch whorl, at which point three varices (per whorl) develop. In *Microrhytis*, on the early teleoconch whorls there are about 12 small lamellar varices, which on about the fifth teleoconch whorl reduce in number to three per whorl. Although previously considered as a subgenus of *Ceratostoma* because of the large denticulate aperture and strong intervarical nodes (Vokes, 1989b, p. 113), work on the western Atlantic species demonstrated the strong resemblance of the early whorls in *Microrhytis* to those in *Pterorytis* and we have concluded that Emerson's original placement is a more accurate assessment of the relationship of the group.

PTERORYTIS (MICRORHYTIS) CHRISTOPHERI Gibson Smith and Gibson Smith MS, n. sp.

Plate 12, figures 1-3

Description: Teleoconch of six to seven whorls; protoconch missing in all material. Outer shell layer of translucent tan calcite, inner layer creamy white aragonite, causing severe decortication in most specimens. Axial sculpture on earliest whorls of about 12 equi-spaced lamel-

lae; by third teleoconch whorl every third lamella becoming a small varix, the two intermediate remaining as small riblets; by fourth whorl, one riblet disappearing, leaving one strong intervarical node between each of three foliaceous varices per whorl. Spiral sculpture beginning with a strong peripheral cord adjacent to anterior suture and a weaker cord at shoulder. On body whorl nine or ten primary spiral cords, with numerous secondary and tertiary intercalated threads; axial growth lamellae rendering these extremely scabrous in intervarical area. Varical margins scalloped by major spiral cords, especially on abapertural side; adapertural side of varices fimbriated by multiple laminae. Suture deeply impressed. Aperture broadly ovate, inner lip smooth; inner side of outer lip with six or seven small denticles, and a long, rectangular labral tooth located at juncture of body whorl and siphonal canal, causing a strong infolding of outer margin of terminal varix. Siphonal canal short, broad, recurved dorsally, sealed over by a plate of shelly material extending from columellar side of canal.

Holotype: NMB H-17659; height 42.1 mm, diameter 26.9 mm.

Type locality: NMB 17516, Cantaure Formation (lower beds); Paraguaná Peninsula, Falcón State, Venezuela (= TU 1269).

Paratype A: NMB H-17663; height 26.9 mm, diameter 15.7 mm.

Paratype B: NMB H-17660; height 26.2, diameter 16.3 mm.

Locality of both, same as holotype.

Etymology of name: For Christopher Gibson Smith, Ph.D., of Guilford, Surrey, England, son of Mr. and Mrs. Jack Gibson Smith, Surrey, England, the collectors.

Occurrence: Cantaure Formation, Venezuela.

Figured specimens: Fig. 1, NMB H-17659 (holotype). Fig. 2, NMB H-17663 (paratype A). Fig. 3, NMB H-17660 (paratype B).

Discussion: In the Gibson Smith Collection of material from the Cantaure Formation of the Paraguaná Peninsula, Venezuela, now in the collections of the Naturhistorisches Museum, Basel, Switzerland, there are 15 specimens of a species recognized long ago by the Gibson Smiths as new, which they intended to name *christopheri,* in honor of their son. It gives us pleasure to publish this taxon, first identified by this astute pair of paleontologists.

Pterorytis (Microrhytis) christopheri, n. sp., bears a strong resemblance to the Early and Middle Miocene Floridian *P.(M.) dryas* (Gardner). Like *P. dryas*, the immature shells are more elaborately ornamented than the adult, but unlike *P. dryas*, in the adult shell the abapertural faces of *P. christopheri* are markedly crenulated by the spiral cords in contrast to the almost flat abapertural surface in *P. dryas*. The aperture of *P. christopheri* is larger, more broadly ovate than that of *P. dryas*, and lacks the posteriormost labral denticle, which in *P. dryas* forms an anal channel.

From both *P. dryas* and the younger *P. ecuadorius* (Vokes), *P. christopheri* differs in having a more inflated body whorl, with

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PLATE 8

Figures Page

1-7. *Pterorytis (Pterorytis) fluviana* Dall 94

1. (X 2) USNM 114122; height 22.5 mm, diameter 14.0 mm.
   Locality: USGS 2280, Natural Well, Duplin County, North Carolina (= TU 376); Duplin Formation.
2. (X 1 1/2) USNM 488728; height 32.0 mm, diameter 20.8 mm.
   Locality: TU 1022; "James City Formation."
3. (X 1 1/2) Stephens Collection; height 45.0 mm, diameter 25.0 mm.
   Locality: TU 1022; "James City Formation."
4. (X 2) USNM 488729; height 24.0 mm, diameter 15.2 mm.
   Locality: TU 558; Waccamaw Formation.
5. (X 2) USNM 488730; height 25.5 mm, diameter 18.2 mm.
   Locality: Calabash, North Carolina (Campbell Coll.); Waccamaw Formation.
6. (X 2) USNM 488731; height 32.4 mm, diameter 19.6 mm.
   Locality: TU 870; Waccamaw Formation.
7. (X 10) UF 20435; height 12.5 mm, diameter 6.0 mm.
   Locality: TU 558; Waccamaw Formation.

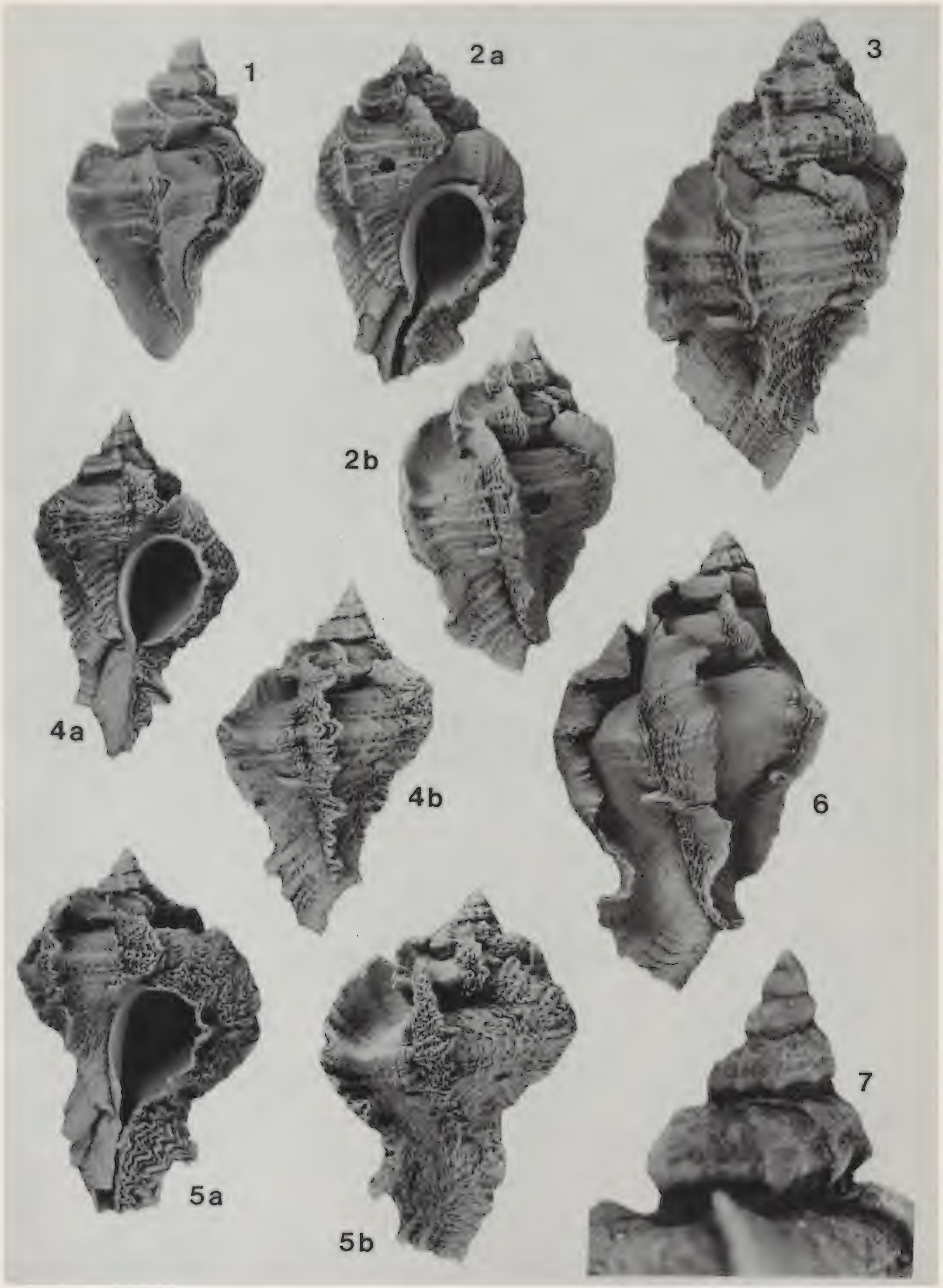

PLATE 8

stronger intervarial nodes. From both species it also differs in having an extremely long labral tooth, which is squared off at the terminal end rather than pointed.

The species of *Microrhytis* nearest in age to *P. christopheri* is *P.(M.) pecki* (Emerson), from the Middle Miocene of Veracruz, Mexico; however, this species bears the least resemblance to *P. christopheri*. The Mexican species is lower spired, with relatively inconspicuous varices, and the labral tooth, as in the other younger species is small and pointed.

PTERORYTIS (MICRORHYTIS) DRYAS (Gardner)

Plate 13, figures 1-3

Pteropurpura dryas GARDNER, 1947, U.S. Geol. Survey, Prof. Paper 142-H, p. 525, pl. 53, fig. 9.

[Ceratostoma] dryas (Gardner). VOKES, 1971, Bulls. Amer. Paleontology, v. 61, no. 268, p. 121.

Description: "Shell rather small for the group, stout, trivaricate, the maximum diameter falling behind the median horizontal. Aperture decidedly more than half as long as the entire shell. Whorls of spire inflated, obtusely angulated at the periphery, rapidly increasing in diameter. Body whorl relatively large, constricted at the base, rendered somewhat cuneate by the axial varices. Whorls of conch probably 6, closely appressed, separated by impressed linear sutures, undulated by the varices of both the whorl in front of the suture and that behind it. Protoconch not preserved but certainly small. Earliest whorl of conch sculptured with 9 subequal and equi-spaced axial ribs, the number gradually diminishing with the growth of the shell and the character changing; final whorl of spire and body triangulated by 3 rather broad, foliated flanges, the terminal flange the broadest of the 3, the dozen or more component laminae visible on the front of the varix; varix crenulated by the spiral sculpture and produced backward on the preceding whorl almost or quite to the periphery; intervarical rib on the later whorls reduced to a rather prominent peripheral tubercle. Spirals obscure and irregular, increasing in number and prominence with the growth of the shell; early whorls usually sculptured with 2 low, rounded lirations, the anterior the more prominent and outlining the obscure peripheral angle; posterior spiral on the later whorls of the type indicated chiefly by the outline of the margin of varices; a third spiral introduced directly behind the suture on the last whorl in the spire becoming on the body, almost but not quite so prominent as the peripheral spiral; 2 or 3 less prominent lirations on the base of the body and irregular secondaries intercalated in the much wider interspaces. Lirae on the anterior fasciole obscure. Aperture oblique, pyriform, broadly rounded behind. Outer lip varicated, the edge of the labral portion of the peristome broadly rounded and crenulated in harmony with the primary spirals; half a dozen obtuse denticles developed a short distance within the margin. Labium feebly convex, reinforced. Pillar sharply rounded and flexed at the entrance to the canal. Anterior canal less than half as long as the aperture including the canal, very narrow, with a backward twist, the margins parallel and proximate but not in contact. Anterior fasciole sharply differentiated, truncate at its extremity, the former fascioles, one to each varix, diverging slightly from the final fasciole." (Gardner, 1947)

Holotype: USNM 371855; height 29 mm, diameter 20 mm.

Type locality: USGS 5630, Oak Grove Sand;

PLATE 9

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1-5. *Pterorytis (Pterorytis) fluviana* Dall 94

1. (X 1 1/2) Stephens Collection; height 37.4 mm, diameter 25.0 mm. Locality: TU 1512; Caloosahatchee Formation.
2. (X 1 1/2) Stephens Collection; height 36.0 mm, diameter 21.2 mm. Locality: TU 1512; Caloosahatchee Formation.
3. (X 4; X 10) Stephens Collection; height 12.8 mm, diameter 9.0 mm. Locality: TU 1512; Caloosahatchee Formation.
4. (X 1 1/2) USNM 488732; height 32.1 mm, diameter 22.1 mm. Locality: TU 768; Caloosahatchee Formation.
5. (X 1 1/4) Stephens Collection; height 45.5 mm, diameter 33.2 mm. Locality: TU 1000; (?) Caloosahatchee Formation.

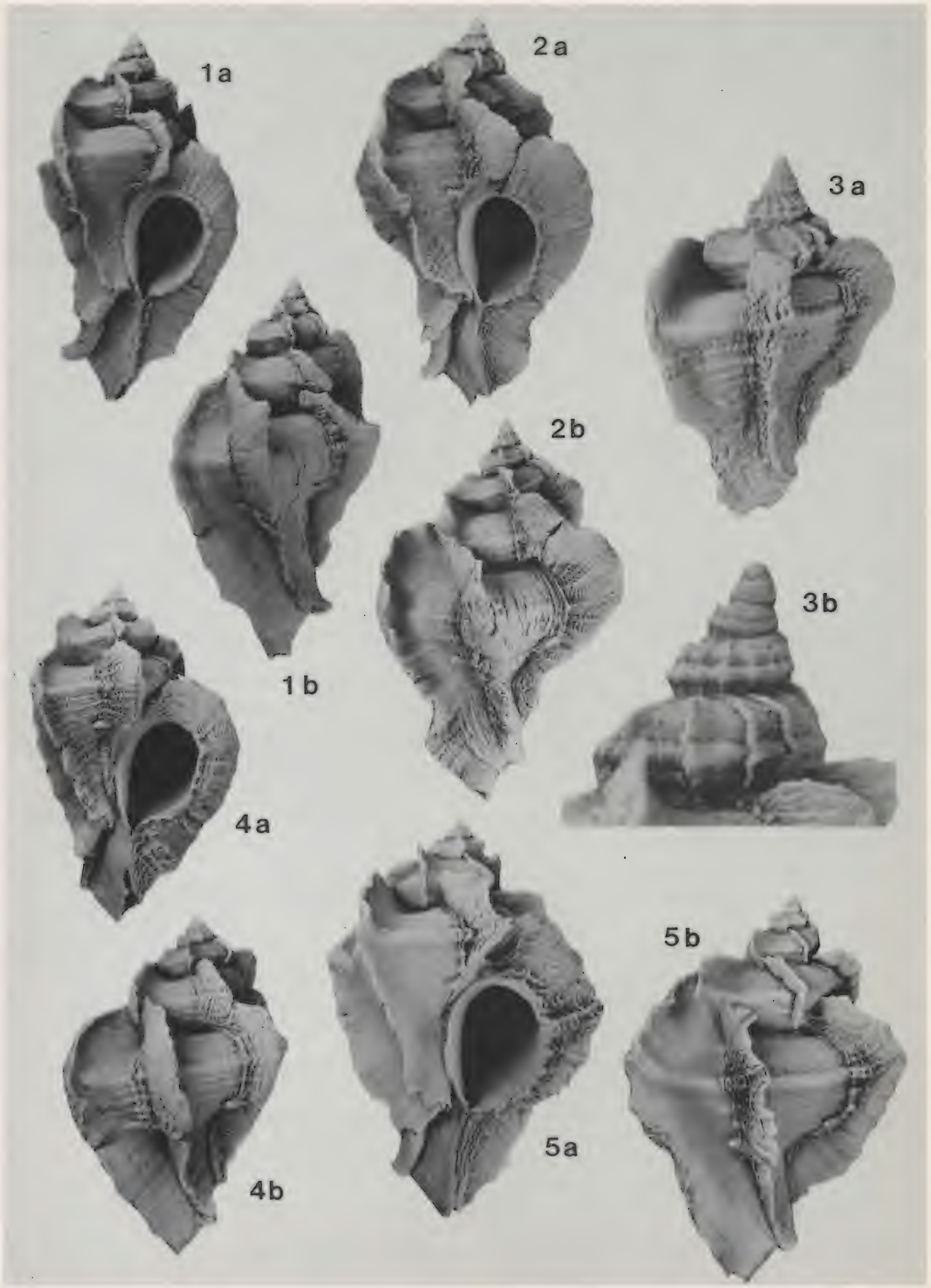

PLATE 9

100 yards below Oak Grove bridge, Yellow River, Okaloosa County, Florida (= TU 91).

Occurrence: Oak Grove Sand and Shoal River Formation, Florida; (?)Thomonde Formation, Haiti.

Figured specimens: Fig. 1, Murray Collection; height 17.2 mm, diameter 11.8 mm; locality UF-WL004 (? = TU 69A). Fig. 2, USNM 488739; height 14.8 mm, diameter 8.8 mm, locality TU 91. Fig. 3, USNM 481847; height 18.1 mm, diameter 12.4 mm; locality USGS 9908, Las Cahobas, Haiti.

Discussion: The northern *P. dryas*, as discussed above, is most similar to the Venezuelan *P. christopheri*, n. sp., but differs in having a less ornamented shell and a more narrow aperture with a smaller labral tooth. From its contemporary southern relative, *P. pecki* Emerson, *P. dryas* differs in having a higher spire, a more impressed suture giving rise to more rounded whorls, and a larger size. Evidently both latter species preferred a shallow, sandy environment, as we have specimens of *P. dryas* from both the Oak Grove Sand and the Shoal River Formation, but none from the Chipola Formation.

In the collections of the U.S. National Museum of Natural History, in material collected in the Thomonde Formation at Las Cahobas, Haiti, by Woodring *et al.* (1924) there is an example of what seems to be this species (pl. 13, fig. 3). In the same beds there is an example of another Shoal River muricid, *Chicoreus (Phyllonotus) aldrichi* (Gardner) (see Vokes, 1990, p. 63, pl. 9, fig. 12), and these Haitian beds seem to be correlative with those of the Shoal River.

PTERORYTIS (MICRORHYTIS) PECKI Emerson
Plate 12, figure 4

Pterorytis n. sp. DURHAM *et al.*, 1955, Geol. Soc. Amer., Bull., v. 66, p. 984.

Pterorytis (Microrhytis) pecki EMERSON, 1959, Amer. Mus. Novitates, no. 1974, p. 6, fig. 4; EMERSON, 1985, Nautilus, v. 99, no. 1, p. 16.

[Ceratostoma] pecki (Emerson). VOKES, 1971, Bulls. Amer. Paleontology, v. 61, no. 268, p. 125.

Ceratostoma (Microrhytis) pecki (Emerson). VOKES, 1989, Tulane Stud. Geol. Paleont., v. 22, no. 4, p. 113.

Description: "Shell small for the genus, with four plus, post-nuclear whorls, nuclear whorls not preserved. Spire small, less than one-third of the height of shell. Body whorl ornamented with three prominent, rib-like varices and a low, rounded nodule centrally located on the weakly spirally sculptured intervarical surface. Ventral surface of varices minutely foliated; single apertural spine preserved on varices of body whorl. Aperture subovate, commonly closed, interior of outer lip with pustules or lirations. Apertural tooth small." (Emerson, 1959)

Holotype: UCMP 37690; height 23.0 mm, diameter 16.0 mm.

PLATE 10

Figures Page

1-8. *Pterorytis (Pterorytis) fluviana* Dall 94

1. (X 1 1/2) USNM 488733; height 35.4 mm, diameter 24.7 mm. Locality: TU 728; Pinecrest beds.
2. (X 1 1/2) USNM 488734; height 36.9 mm, diameter 22.1 mm. Locality: TU 729; Pinecrest beds.
3. (X 1 1/2) USNM 488735; height 32.4 mm, diameter 22.5 mm. Locality: TU 729; Pinecrest beds.
4. (X 1 1/2) USNM 488736; height 37.2 mm, diameter 21.0 mm. Locality: TU 729; Pinecrest beds.
5. (X 1 1/2) USNM 488737; height 32.5 mm, diameter 19.2 mm. Locality: TU 729; Pinecrest beds.
6. (X 1 1/2) Stephens Collection; height 39.4 mm, diameter 25.7 mm. Locality: TU 1000; Pinecrest beds.
7. (X 1 1/4) USNM 488738; height 42.8 mm, diameter 27.7 mm. Locality: TU 729; Pinecrest beds.
8. (X 1 1/2) Stephens Collection; height 31.9 mm, diameter 19.8 mm. Locality: TU 729; Pinecrest beds.

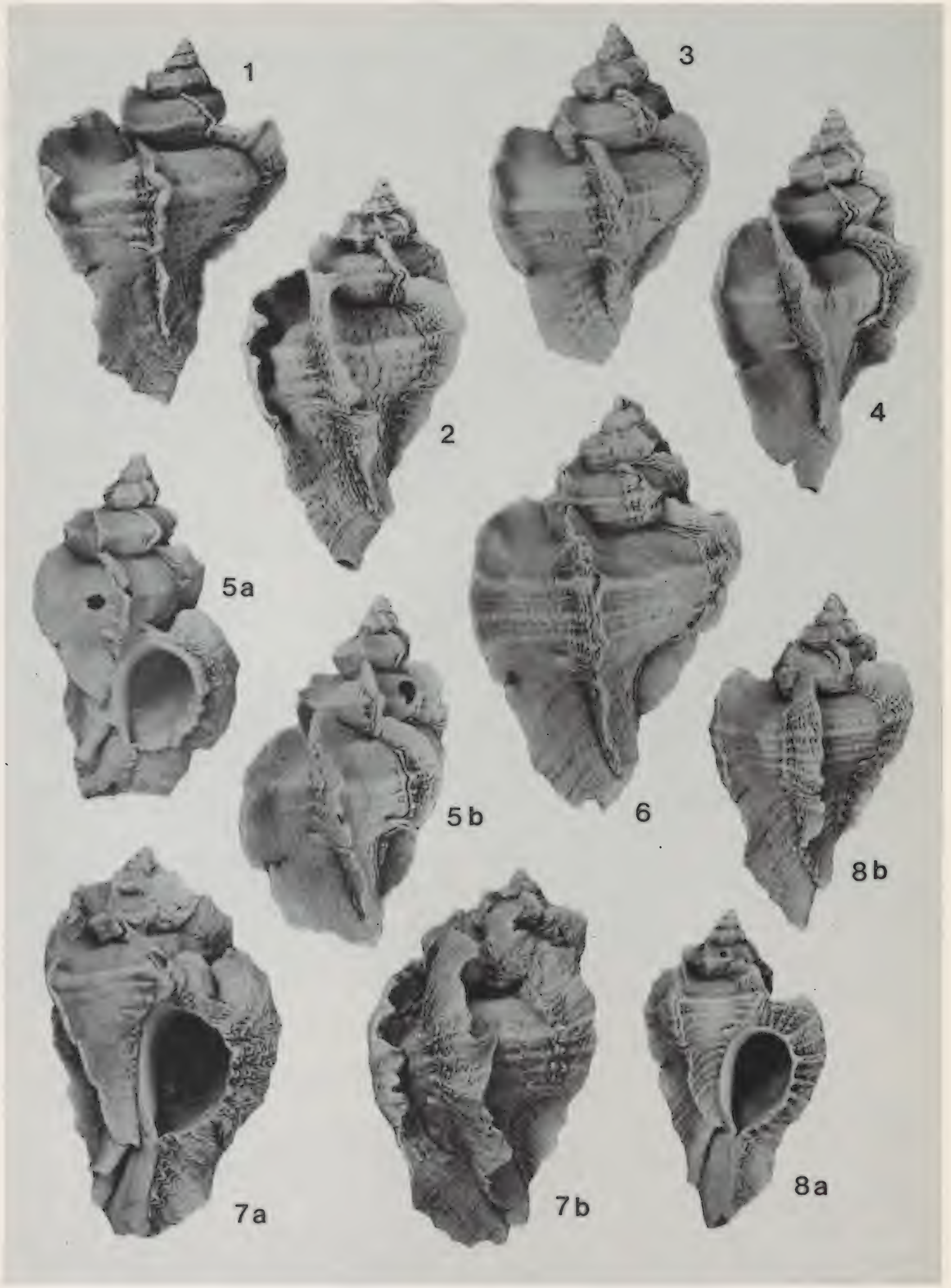

PLATE 10

Type locality: UCMP locality A-8125, unnamed formation; road-cut along Trans-isthmian highway from Salina Cruz to Coatzocoales [Coatzacoalcos], about 2.6 km south of Rio Jaltepec, Veracruz, Mexico (= TU 636).

Occurrence: Unnamed formation, Veracruz/Oaxaca line, Mexico.

Figured specimen: UCMP 37691 (paratype); height 22.8 mm, diameter 15.7 mm; locality UCMP A-8124 (= TU 635). Other occurrence: TU locality 635.

Discussion: As was noted by Vokes (1989b, p. 114), the locality for the holotype and paratypes of *P.(M.) pecki* (UCMP A-8125 and A-8124 = TU 636 and TU 635, respectively) have been dated as Neogene Zone N.13-N.14, or Middle Miocene in age. The molluscan assemblage at these localities consists of extremely shallow-water material, including a fair bit of gravel, together with a good planktic foraminiferal fauna, indicating a gravity-flow of probably intertidal material into the deeper environment.

PTERORYTIS (MICRORHYTIS) ECUADORIUS (Vokes)
Plate 13, figures 4-6

Ceratostoma (Microrhytis) ecuadorium VOKES, 1989, Tulane Stud. Geol. Paleont., v. 22, no. 4, p. 113, pl. 1, figs. 3, 4.

Description: "Shell of average size, probably six teleoconch whorls in adult; protoconch unknown. Spiral ornamentation on early teleoconch whorls of two strong cords, which persist up to the body whorl, where they form one weaker cord at the shoulder and another somewhat stronger cord just anterior to it. These supplemented by a third cord near base of the body whorl and numerous weaker threads between, and anterior to, the three major cords. Axial ornamentation on earliest whorls of approximately 12 small lamellar varices, crenulated by spiral cords; gradually reducing in number until on approximately the fifth teleoconch whorl becoming three varices with one strong intervarical node between each pair. Varices fimbriated on adapertural face, slightly recurved abaperturally, with a weak fold at shoulder. In addition to varices, the shell surface shagreened by numerous axial growth lines. At juncture of body whorl and siphonal canal a sharp adaperturally directed labral tooth, causing the varix to be enfolded behind it. Aperture large, ovate; columellar lip smooth, adnate posteriorly, free-standing anteriorly. Inner side of outer lip with approximately seven strong elongate denticles. Siphonal canal moderately long, wide, sealed over by an extension of shell material from columellar side; distal end slightly recurved." (Vokes, 1989)

Holotype: USNM 445399; height 23.2 mm, diameter 15.5 mm.

Type locality: TU 1507, Angostura Formation; Punta Verde, large point just east of Río Verde, or about 30 km east of Río Esmeraldas, Province of Esmeraldas, Ecuador.

Occurrence: Angostura Formation, Ecuador; Gatun Formation, Panama.

Figured specimens: Fig. 4, USNM 488740; height 37.2 mm, diameter 22.2 mm; locality TU 757. Fig. 5, USNM 488741; height 32.5 mm, diameter 18.5 mm; locality TU 757. Fig. 6, USNM 445400 (paratype); height 26.8 mm, diameter 16.9 mm; locality TU 1507.

Discussion: Two specimens from the Late Miocene Gatun Formation of Panama prove to be the same as a species described from the Pacific coast of Ecuador, in the Angostura Formation, which is correlative with the Gatun Formation. The only other species to which *P. ecuadorius* has a close resemblance is the slightly older and presumably ancestral *P. dryas*, which differs in having somewhat more pronounced spiral sculpture and a smaller labral tooth. It bears much less resemblance to the geographically closer Early Miocene *P.(M.) christopheri*, n. sp., which is assumed to have lived in a slightly deeper environment than *P. dryas* and *P. ecuadorius*.

V. LOCALITY DATA

The following are Tulane University fossil locality numbers:

60. Jackson Bluff Fm., borrow pits at Jackson Bluff, Ochlockonee River (NW 1/4 Sec. 21, T1S, R4W), Leon Co., Florida.
68. Caloosahatchee Fm., North St. Petersburg, 70th Ave. at 9th St. N., Pinellas Co., Florida.
69A. Shoal River Fm., first ravine upstream from Shell Bluff, Shoal

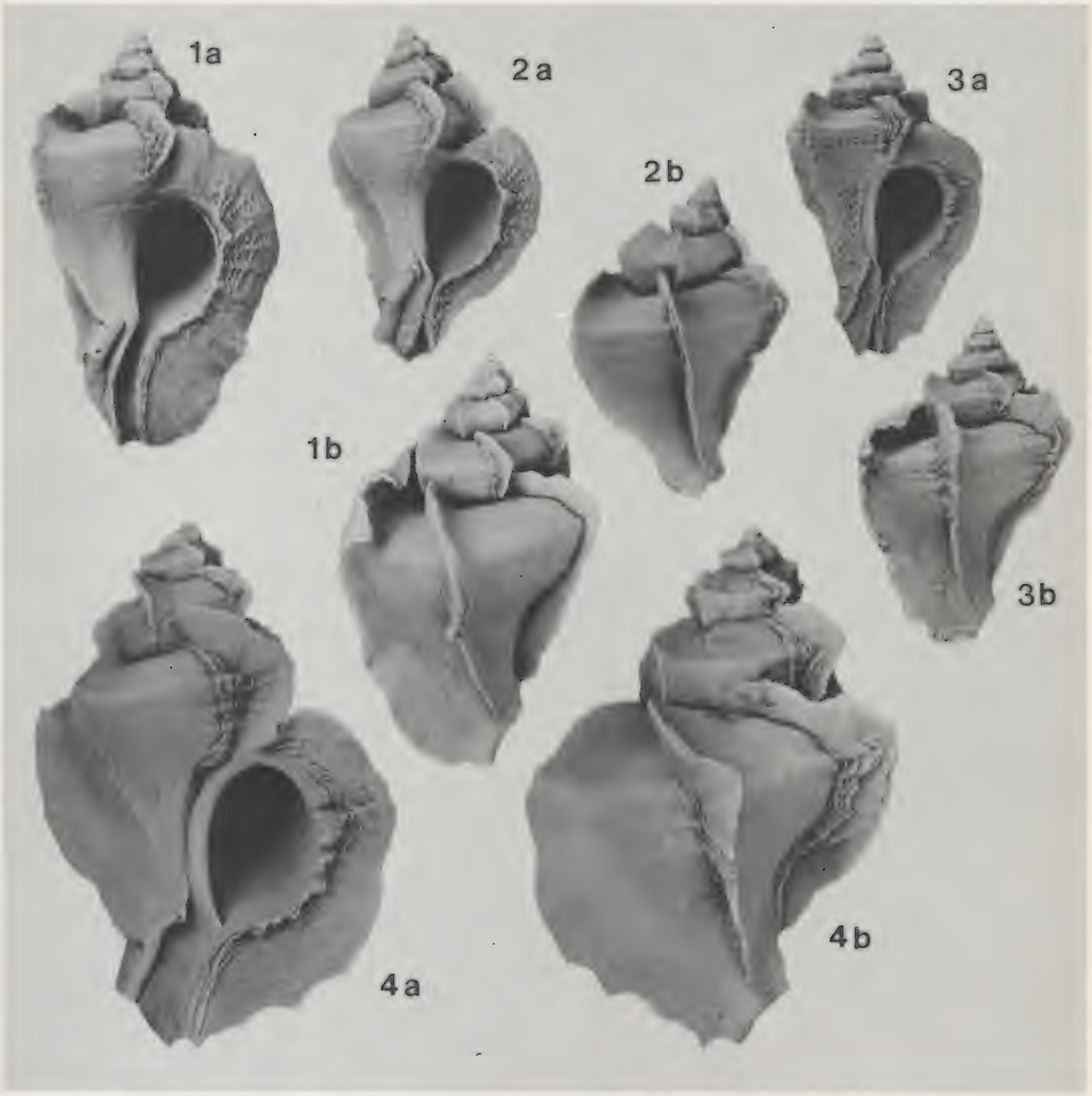

PLATE 11

Figures Page

1-4. *Pterorytis (Pterorytis) roxaneae* Petuch 100

1. (X 1 1/2) Stephens Collection; height 34.2 mm, diameter 21.6 mm. Locality: TU 1524; uppermost Pinecrest beds.
2. (X 1 1/2) Stephens Collection; height 27.1 mm, diameter 18.4 mm. Locality: TU 1524; uppermost Pinecrest beds.
3. (X 1 1/2) Stephens Collection; height 26.1 mm, diameter 17.6 mm. Locality: TU 1524; uppermost Pinecrest beds.
4. (X 1 1/4) Stephens Collection; height 51.0 mm, diameter 36.0 mm. Locality: TU 1000; uppermost Pinecrest beds.

River (NW 1/4 Sec. 4, T3N, R21W), about 3 1/2 miles north of Mossyhead, Walton Co., Florida.

91. Oak Grove Sand, type locality, west bank of Yellow River, about 100 yards below bridge at Oak Grove (NE 1/4 Sec. 20, T5N, R23W), Okaloosa Co., Florida.

376. Duplin Fm., "Natural Well," sinkhole on Matthews' farm, on North Carolina Highway 1003, 2 miles southwest of Magnolia, Duplin Co., North Carolina.

457. Chipola Fm., west bank of Chipola River, about 1/2 mile below Tenmile Creek (SW 1/4 Sec. 17, T1N, R9W), Calhoun Co., Florida.

458. Chipola Fm., east bank of Chipola River, above Farley Creek (SW 1/4 Sec. 20, T1N, R9W), Calhoun Co., Florida.

459. Chipola Fm., east bank of Chipola River, steep bank about 1500 feet above the mouth of Taylor Lake Branch (NW 1/4 Sec. 29, T1N, R9W), Calhoun Co., Florida.

520. Pinecrest beds, spoil banks, canal 0.9 mile east of Brighton on Florida Highway 70 (Sec. 25, T37S, R32E), Highlands Co., Florida.

523. Pinecrest beds, Harney Pond Canal spoil banks, 6 miles northwest of Florida Highway 78, Brighton Indian Reservation (NW 1/4 Sec. 22, T39S, R32E), Glades Co., Florida.

534. Tamiami Fm., spoil bank at Port Charlotte Baptist Church, about 1/2 mile north of U.S. Highway 41, on road 1 1/2 miles southeast of Murdock (NE 1/4 Sec. 8, T40S, R22E), Charlotte Co., Florida.

539B. Caloosahatchee Fm., Shell Creek (lower beds), about 8 miles east of Cleveland (Sec. 30, T40S, R25E), Charlotte Co., Florida.

546. Chipola Fm., Tenmile Creek, about 1 3/4 miles west of Chipola River (NE 1/4 Sec. 12, T1N, R10W), Calhoun Co., Florida.

547. Chipola Fm., west bank of Chipola River, about 2000 ft. above Fourmile Creek (SW 1/4 Sec. 29, T1N, R9W), Calhoun Co., Florida.

548. Chipola Fm., west bank of Chipola River, at bend about 1800 feet south of mouth of Farley Creek (NW 1/4 Sec. 29, T1N, R9W), Calhoun Co., Florida.

549. Chipola Fm., east bank of Chipola River, about 1/4 mile below Fourmile Creek (NE 1/4 Sec. 32, T1N, R9W), Calhoun Co., Florida.

554. Chipola Fm., east bank of Chipola River at power line crossing (SW 1/4 Sec. 17, T1N, R9W), Calhoun Co., Florida.

555. Chipola Fm., east bank of Chipola River, about 1000 ft. above Fourmile Creek (SW 1/4 Sec. 29, T1N, R9W), Calhoun Co., Florida.

558. Waccamaw Fm., borrow pits at north end of Crescent Beach Airport, Crescent Beach, Horry Co., South Carolina.

559. Waccamaw Fm., "Neill's Eddy Landing," south bank of Cape Fear River near Acme, Columbus Co., North Carolina.

562. Haywood Landing Member, Belgrade Fm. [= "Silverdale beds"], Onslow County marl pit, on south side of Webb Creek, near

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PLATE 12

Figures Page

1-3. *Pterorytis (Microrhytis) christopheri*, n. sp. 101

1. (X 1 1/2) NMB H-17659 (holotype); height 42.1 mm, diameter 26.9 mm. Locality: NMB 17516, Paraguaná Peninsula, Falcón State, Venezuela (= TU 1269); Cantaure Formation.
2. (X 2) NMB H-17663 (paratype A); height 26.9 mm, diameter 15.7 mm.
3. (X 2) NMB H-17660 (paratype B); height 26.2 mm, diameter 16.3 mm. Locality of both: same as holotype.

4. *Pterorytis (Microrhytis) pecki* Emerson 106

(X 2) UCMP 37691 (paratype); height 22.8 mm, diameter 15.7 mm. Locality: UCMP locality A-8124, about 2.3 km south of Río Jaltepec, Veracruz, Mexico (= TU 635); unnamed formation.

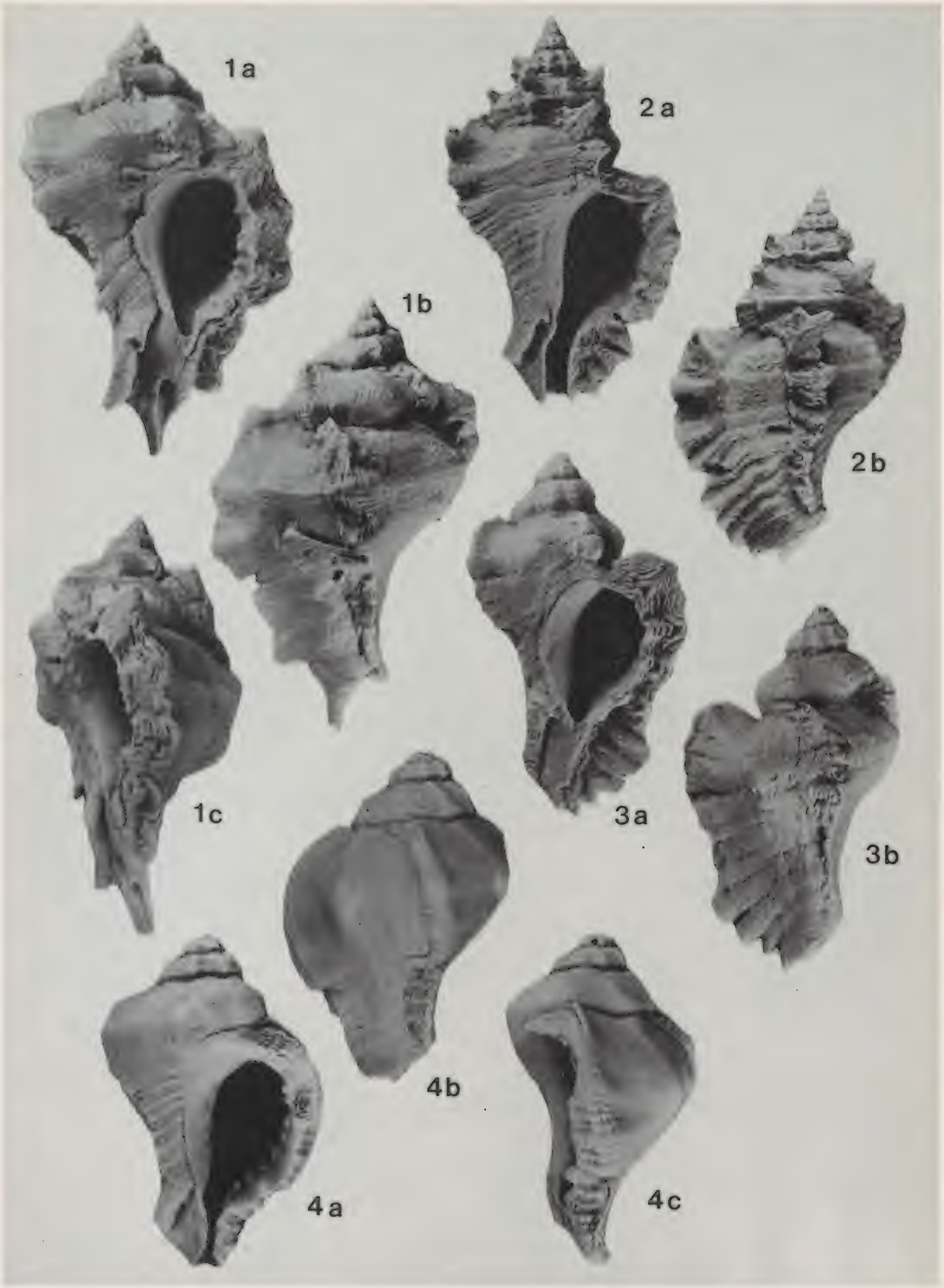

PLATE 12

Silverdale, Onslow Co., North Carolina.
613. Yorktown Fm., Rice's marl pit, Harris Creek Road, Hampton, York Co., Virginia.
635. Unnamed formation, roadcut on Mexico Highway 185, 1.4 miles (2.3 km) south of bridge over Río Jaltepec, at Oaxaca-Veracruz state line, Mexico (= University of California, Museum of Paleontology locality A-8124).
636. Unnamed formation, roadcut on Mexico Highway 185, 1.5 miles (2.4 km) south of bridge over Río Jaltepec, at Oaxaca-Veracruz state line, Mexico (= University of California, Museum of Paleontology locality A-8125).
708. Chipola Fm., at small waterfall on tributary to Tenmile Creek, south bank, about 1/4 mile downstream from bridge of Florida Highway 73 (NW 1/4 Sec. 12, T1N, R10W), Calhoun Co., Florida.
726. Caloosahatchee Fm., Hendry County rock pit, 1/2 mile north of Florida Highway 80, three miles west of La Belle (SE 1/4 Sec. 14, T43S, R28E), Hendry Co., Florida.
728. Pinecrest beds, spoil banks on west side of Kissimmee Canal and east side of Kissimmee River, just across from U.S. Corps of Engineers Structure 65-D (Sec. 33, T36S, R33E), Okeechobee Co., Florida.
729. Pinecrest beds, spoil banks on west side of Kissimmee Canal and east side of Kissimmee River, approximately 1/2 mile south of U.S. Corps of Engineers Structure 65-D (S 1/2 Sec. 33, T36S, R33E), Okeechobee Co., Florida.
730. Pinecrest beds, embankment of Seaboard Airline Railroad, just west of Kissimmee River (NW 1/4 Sec. 20, T36S, R33E), Highlands Co., Florida.
757. Gatun Fm., roadcut on south side of Boyd-Roosevelt Highway at junction of road to "Refinería Panamá, S.A.," just east of Cativa, Prov. of Colón, Panama.
759. Bermont Fm., spoil banks north side of Caloosahatchee River, 2 miles west of Ortona Lock (NE 1/4 Sec. 29, T42S, R30E), Glades Co., Florida.
767. Caloosahatchee Fm. and Bermont Fm. mixed, spoil banks north side of Caloosahatchee River, 5 miles west of Ortona Lock (NW 1/4 Sec. 36, T42S, R29E), Glades Co., Florida.
768. Caloosahatchee Fm. and Bermont Fm. mixed, spoil banks north side of Caloosahatchee River, 5 1/2 miles west of Ortona Lock (NW 1/4 Sec. 35, T42S, R29E), Glades Co., Florida.
769. Pinecrest beds, spoil banks east side of Kissimmee River, 1 1/2 to 2 miles south of U.S. Corps of Engineers Structure 65-D (NE 1/4 Sec. 35, T36S, R33E), Okeechobee Co., Florida.
770. Pinecrest beds and Caloosahatchee Fm. mixed, spoil banks west side of Kissimmee River, 1 1/2 to 3 1/2 miles north of Florida Highway 70 (Secs. 10, 14, 15, and 28, T37S, R33E), Highlands Co., Florida.
787. Chipola Fm., Tenmile Creek, about 1 1/2 miles west of Chipola River (SE 1/4 Sec. 12, T1N, R10W), Calhoun Co., Florida.

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Figures Page

1-3. *Pterorytis (Microrhytis) dryas* (Gardner) 104
1. (X 3) Murray Collection; height 17.2 mm, diameter 11.8 mm.
Locality: UF-WL004 (? = TU 69A); Shoal River Formation.
2. (X 3) USNM 488739; height 14.8 mm, diameter 8.8 mm.
Locality: TU 91; Oak Grove Sand.
3. (X 3) USNM 481847; height 18.1 mm, diameter 12.4 mm.
Locality: USGS 9908, Las Cahobas, Haiti; Thomonde Formation.

4-6. *Pterorytis (Microrhytis) ecuadorius* (Vokes) 108
4. (X 1 1/2) USNM 488740; height 37.2 mm, diameter 22.2 mm.
Locality: TU 757; Gatun Formation.
5. (X 1 1/2) USNM 488741; height 32.5 mm, diameter 18.5 mm.
Locality: TU 757; Gatun Formation.
6. (X 2) USNM 445400 (paratype); height 26.8 mm, diameter 16.9 mm.
Locality: TU 1507; Angostura Formation.

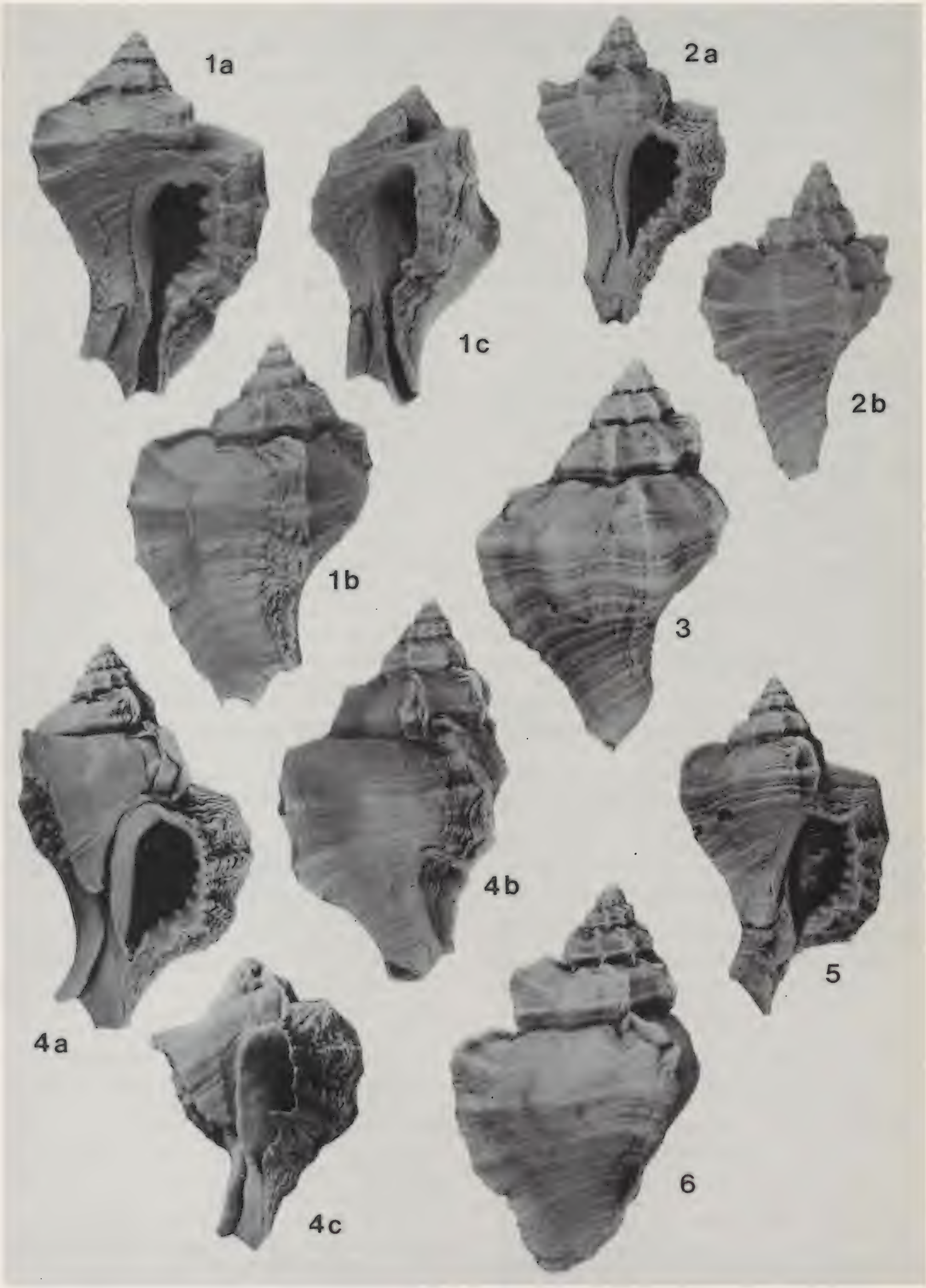

PLATE 13

789. Tamiami Fm., north side of Caloosahatchee River, 0.3 mile east of old lock (NW 1/4 Sec. 30, T42S, R30E), Glades Co., Florida.
796. Pinecrest beds, material exposed during construction of "Alligator Alley," 12.8 miles east of Florida Highway 29 (T49S, R32E), Collier Co., Florida.
797. Pinecrest beds, material exposed during construction of "Alligator Alley," 13.3 miles east of Florida Highway 29 (T49S, R32E), Collier Co., Florida.
806. Chipola Fm., west bank of Chipola River, about 1/2 mile below power line crossing (NW 1/4 Sec. 20, T1N, R9W), Calhoun Co., Florida.
807. Chipola Fm., west bank of Chipola River, about 1/4 mile below power line crossing (NW 1/4 Sec. 20, T1N, R9W), Calhoun Co., Florida.
817. Chipola Fm., south side of Tenmile Creek, large gully on the property of Mr. A. Sexton (1967) (SE 1/4 Sec. 12, T1N, R10W), Calhoun Co., Florida.
818. Chipola Fm., Farley Creek, 0.1 mile west of bridge of Florida Highway 275 (SW 1/4 Sec. 21, T1N, R9W), Calhoun Co., Florida.
819. Chipola Fm., Farley Creek, 0.2 mile west of bridge of Florida Highway 275 (SW 1/4 Sec. 21, T1N, R9W), Calhoun Co., Florida.
820. Chipola Fm., Farley Creek, at bridge of Florida Highway 275 (SW 1/4 Sec. 21, T1N, R9W), Calhoun Co., Florida.
821. Chipola Fm., Farley Creek, 0.1 mile east of bridge of Florida Highway 275 (SW 1/4 Sec. 21, T1N, R9W), Calhoun Co., Florida.
823. Chipola Fm., Farley Creek, about 2000 feet east of bridge of Florida Highway 275 (SE 1/4 Sec. 21, T1N, R9W), Calhoun Co., Florida.
824. Chipola Fm., Farley Creek, about 1/2 mile east of bridge of Florida Highway 275 (SE 1/4 Sec. 21, T1N, R9W), Calhoun Co., Florida.
825. Chipola Fm., Farley Creek at abandoned mill about 1/4 mile west of bridge of Florida Highway 275 (SW 1/4 Sec. 21, T1N, R9W), Calhoun Co., Florida.
828. Chipola Fm., Farley Creek, just upstream from mouth of unnamed tributary about 3/4 mile downstream from bridge of Florida Highway 275 (SE 1/4 Sec. 20, T1N, R9W), Calhoun Co., Florida.
830. Chipola Fm., Tenmile Creek, at power line crossing about 1 mile west of Chipola River (SE 1/4 Sec. 12, T1N, R10W), Calhoun Co., Florida.
831. Chipola Fm., Tenmile Creek [lowest beds exposed], slightly less than one mile west of Chipola River (SW 1/4 Sec. 7, T1N, R9W), Calhoun Co., Florida.
842. Yorktown Fm., road metal quarry on Virginia Highway 238, 1.4 miles east of U.S. Highway 17 at Yorktown, York Co., Virginia.
855. Yorktown Fm., "Fort Boykins," Burwell's Bay, south bank of James River, one mile west of Mogart's Beach and approximately one mile north of Smithfield, Isle of Wight Co., Virginia.
866. Haywood Landing Member, Belgrade Fm. [= "Silverdale beds"], marl pit on north side of Webb Creek and east side of unnumbered county road, Silverdale, Onslow Co., North Carolina.
870. Waccamaw Fm., pits on east side of North Carolina Highway 130, 2.8 miles north of Old Dock School, Old Dock, Columbus Co., North Carolina.
932. Pinecrest beds, east side of Kissimmee Canal and 1/2 mile south of Seaboard Airline Railroad, south of Fort Basinger (SE 1/4 Sec. 20, T36S, R33E), Okeechobee Co., Florida.
949. Chipola River, west bank about 0.1 mile below power line crossing (SW Sec. 17, T1N, R9W), Calhoun Co., Florida.
950. Chipola Fm., Chipola River, west bank about 2000 feet above Farley Creek (SW 1/4 Sec. 20, T1N, R9W), Calhoun Co., Florida.
951. Chipola Fm., Tenmile Creek, about 1 1/2 miles west of Chipola River (SE 1/4 Sec. 12, T1N, R10W), Calhoun Co., Florida.
977. Unnamed Late Pleistocene formation, mudlump no. 90, mouth of South Pass, Mississippi River delta, Plaquemines Parish, Louisiana.
980. Tamiami Fm., Port Charlotte Development, spoil banks on north side U.S. Highway 41, on canal 3.3 miles northwest of Florida Highway 771 (Sec. 3, T40S, R21E), Charlotte Co., Florida.
998. Chipola Fm., Tenmile Creek, about 1 1/2 miles west of Chipola River (SE 1/4 Sec. 12, T1N, R10W), Calhoun Co., Florida.
999. Chipola Fm., Farley Creek, about 300 yards downstream from bridge of Florida Highway 275 (SW 1/4 Sec. 21, T1N, R9W), Calhoun Co., Florida.
1000. Pinecrest beds, APAC pits at east end of

17th St., about 8 miles east of U.S. Highway 301 at Sarasota [now northwest corner of Fruitville Road exit I-75], (T36S, R19E) Sarasota Co., Florida.

1021. Chipola Fm., small tributary (not shown on USGS topographic map) on east bank of Chipola River about 1/2 mile below power line crossing (NE 1/4 Sec. 20, T1N, R9W), Calhoun Co., Florida.

1022. "James City Fm.", Lee Creek Mine, Texasgulf, Inc., phosphate mine at mouth of Lee Creek, south bank of Pamlico River, near Aurora, Beaufort Co., North Carolina.

1025. Concepcion Inferior Fm., first roadcut on east side of old road from Nueva Teapa to Ixhuatlan, 0.8 km south of junction with highway to Coatzacoalcos [formerly Mexico Highway 180; new Highway 180 parallels this road slightly to the east], Veracruz, Mexico.

1044. Pinecrest beds, spoil banks, west side of L-28 Interceptor Canal, 3 1/2 miles north of junction with Hendry County Highway 833, north side of Big Cypress Indian Reservation (T47S, R33E), Hendry Co., Florida.

1048. Chipola Fm., Farley Creek, about 0.8 mile east of bridge of Florida Highway 275 (NE 1/4 Sec. 21, T1N, R9W), Calhoun Co., Florida.

1050. Chipola Fm., west bank of Chipola River, immediately below power line crossing, and directly across from TU locality 554 (SW 1/4 Sec. 17, T1N, R9W), Calhoun Co., Florida.

1196. Chipola Fm., Farley Creek, about 0.8 mile east of bridge on Florida Highway 275 (NE 1/4 Sec. 21, T1N, R9W), Calhoun Co., Florida.

1269. Cantaure Fm., series of arroyos about 500 meters south of "Casa Cantaure" [which is literally one house and which is about 400 meters south of older, now abandoned, house that was the "Casa Cantaure" of Jung, 1965, and others], 14 km (by road) west of Pueblo Nuevo, Paraguaná Peninsula, Falcón State, Venezuela.

1318. Concepcion Inferior Fm., hillcut on pipeline just to northeast of Campo El Chapo, on old road from Nueva Teapa to Ixhuatlan, 4 km south of old road to Coatzacoalcos [formerly Mexico Highway 180; new Highway 180 parallels this poad slightly to east], Veracruz, Mexico.

1321. Concepcion Inferior Fm., "Kilometer 70," which is K 70 on Trans-Isthmus railroad south of Coatzacoalcos, and 5 km north of Almagres, Veracruz, Mexico

1493. Pinecrest beds, Arvida Pit, on Bird Road (= W. 40th St.), approximately 5 miles west of Florida Turnpike, on west side of Coral Gables, Dade Co., Florida.

1507. Angostura Fm., large point just east of Río Verde, or approximately 30 km east of Río Esmeraldas, Prov. of Esmeraldas, Ecuador.

1512. Pinecrest beds, Caloosahatchee Fm. and Bermont Fm. mixed, DeSoto Shell Company, pits 2 miles east of Florida Highway 31, about 12 miles south of Arcadia (T39S, R25E), DeSoto Co., Florida.

1514. Concepcion Inferior Fm., roadcuts 1.5 km south of old Mexico Highway 180 (now side road into Coatzacoalcos) on new bypass, which is 15 km east of old bridge at Coatzacoalcos, Veracruz, Mexico.

1515. Concepcion Inferior Fm., roadcuts 0.5 km south of intersection of old Mexico Highway 180 (now side road into Coatzacoalcos) on new bypass, which is 15 km east of old bridge at Coatzacoalcos, Veracruz, Mexico.

1524. Pinecrest beds, Quality Aggregate Pit, off Richardson Road, north side of Fruitville Road and east of highway I-75, east of Sarasota, Sarasota Co., Florida.

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VII. APPENDIX: GENUS-GROUP TAXA NOW INCLUDED IN THE OCENEBRINAE

Inasmuch as through the years there has been considerable shuffling about of

the various taxa now considered to be members of the subfamily Ocenebrinae, a complete list of the genus-group taxa presently considered to belong to the subfamily seems desirable. Names are listed in alphabetical order, as infra-taxa relationships are not certain in many cases, and those found only in the fossil record (at this time) are shown in bold face. For full bibliographic references and synonyms for most of these genera the reader is referred to Vokes, 1964.

GROUP I – species with a sealed canal (considered to be Ocenebrinae as of Vokes, 1971); subject of present work.

Calcitrapessa Berry, 1959
Ceratostoma Herrmannsen, 1846
Argyrobessa, n. gen.
Fenolignum, n. gen.
Genkaimurex Kuroda, 1953
Hadriania Bucquoy, Dautzenberg, and Dollfus, 1882
Heteropurpura Jousseaume, 1880
Jaton Pusch, 1837
Microrhytis Emerson, 1959
Miocenebra Vokes, 1963
Ocenebra Leach *in* Gray, 1847
Ocinebrellus Jousseaume, 1880
Ocinebrina Jousseaume, 1880
Odontopurpura, n. subgen.
Poropteron Jousseaume, 1880
Pteropurpura Jousseaume, 1880
Pterorytis Conrad, 1836
n. gen. (for *Murex lugubris* Broderip, 1833)

GROUP II – taxa now included in Ocenebrinae by Kool (1993), Vermeij and Kool (1994), and Vermeij (1995). In addition, a number of monotypic genera known only from the fossil record are questionably included, essentially for lack of a better idea about placement.

Subgroup A: Genera with open canal, and well-defined axial sculpture.

Austrotrophon Dall, 1902
Bedeva Iredale, 1924
Crassilabrum Jousseaume, 1880
Eupleura Adams and Adams, 1853
Forreria Jousseaume, 1880
Leptomurex Woodring, 1973
(?)**Lissomuricopsis** Merle, 1989
(?)**Lyropurpura** Jousseaume, 1880
Mariasalpinx Petuch, 1988
Namamurex Carrington and Kensley, 1969
(?)**Odontopolys** Gabb, 1860
Pterynopsis Vokes, 1973
Roperia Dall, 1898
(?)**Stephanosalpinx** Petuch, 1988
Urosalpinx Stimpson, 1865
Vaughtia Houart, 1995
(?)*Vitularia* Swainson, 1840
Vokesinotus Petuch, 1988
(?)**Yasila** Olsson, 1930
Zacatrophon Hertlein and Strong, 1951

Subgroup B: genera with open canal, predominantly spiral sculpture.

Acanthina Fischer de Waldheim, 1807
Acanthinucella Cooke, 1918
Chorus Gray, 1847
Ecphora Conrad, 1843
Entacanthus von Ihering, 1907
Haustrum Perry, 1811
Lepsiella Iredale, 1912
Nucella Roding, 1798
Spinucella Vermeij, 1993
Trochia Swainson, 1840
(?)**Zulloia** Petuch, 1994
n. gen. (for *Monoceros mirabilis* Moricke, 1896; DeVries and Vermeij, in press)

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A NEW SPECIES OF *CALYPTRAPHORUS* (MESOGASTROPODA:STROMBIDAE) FROM THE MAASTRICHTIAN OF SOUTHERN MEXICO; SOME PALEOBIOGEOGRAPHIC AND EVOLUTIONARY IMPLICATIONS

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I. ABSTRACT

A new species of strombid gastropod is described from the lower Maastrichtian deposits from the Mexcala Formation, Guerrero State, southern México. More than 300 specimens of the new species were collected at one locality. The specimens include all stages of development, from juveniles to adults.

Paleobiogeographic and evolutionary analysis for the genus of this gastropod suggests that it had a wide distribution around the Tethyan Province, and that after the K-T event, the genus migrated northward, until the Eocene, when it became extinct.

II. INTRODUCTION

A diverse, poorly known, and well-preserved Maastrichtian molluscan fauna has been recently restudied from intensive sampling at a few localities from the Upper Cretaceous Mexcala Formation in Guerrero State, southern México. The first report of this fauna included only illustrations, without description, of 15 gastropod species (Alencáster, 1980), some of which were misidentified.

The diversity of groups present at these localities includes planktic and benthic foraminiferans, corals, gastropods, nautiloids, ammonites, bivalves, scaphopods, annelids, crustaceans, echinoids, and vertebrate remains. This material was collected at three outcrops, located 125 km south of México City, and 70 km southeast of Iguala (Fig. 1), near a town locally known as Texmalac.

The lithology consists of light-brown marls, becoming sandier and blue to gray-green toward the top of the sequence, as the abundance and diversity of fossils also decreases. It is interesting to note that several meters above the main localities, gastropods are the only group present, and their sizes are larger compared with samples of the same species at the levels with more abundance.

The Mexcala Formation is very complicated structurally and lithologically. Its outcrop areas include the states of Morelos, México, Guerrero, and Puebla. It was defined by Fries (1960, p. 2), based on the type section proposed by Bohnenberg-Thomas (1955), as a flysch sequence of about 1,220 meters of rhythmic alternation of coarse and fine clastics, with lateral and vertical variations. The Mexcala Formation is extremely folded and faulted at the area of study. It ranges in age from the Turonian, exposed in the central portion of Guerrero State (Bohnenberg-Thomas, 1955; Böse, 1923; Dávila-Alcocer, 1974; González-Arreola, 1977; López-Ramos, 1983; Perrilliat-Montoya, 1974) to the Maastrichtian, exposed to the northeast of Guerrero State (Alencáster, 1980; de Cserna *et al.*, 1980; Ortega-Gutiérrez, 1980).

In a second paper on the Texmalac fauna, Vega and Feldmann (1992) reported a new species of retroplumid crab. In this paper, a more extensive discussion on the paleoenvironment is given, as well as some implications on the paleobiogeographic significance of that genus of crab. Some palynomorphs are also reported, and some were recognized as typical of the paleoflora of South America (Enrique Martínez, pers. comm.). Planktic foraminiferans from the studied localities include *Gansserina gansseri, Rosita fornicata, Globotruncana ventricosa, Globotruncana linneiana, Rugoglobigerina rugosa, Hedbergella mon-*

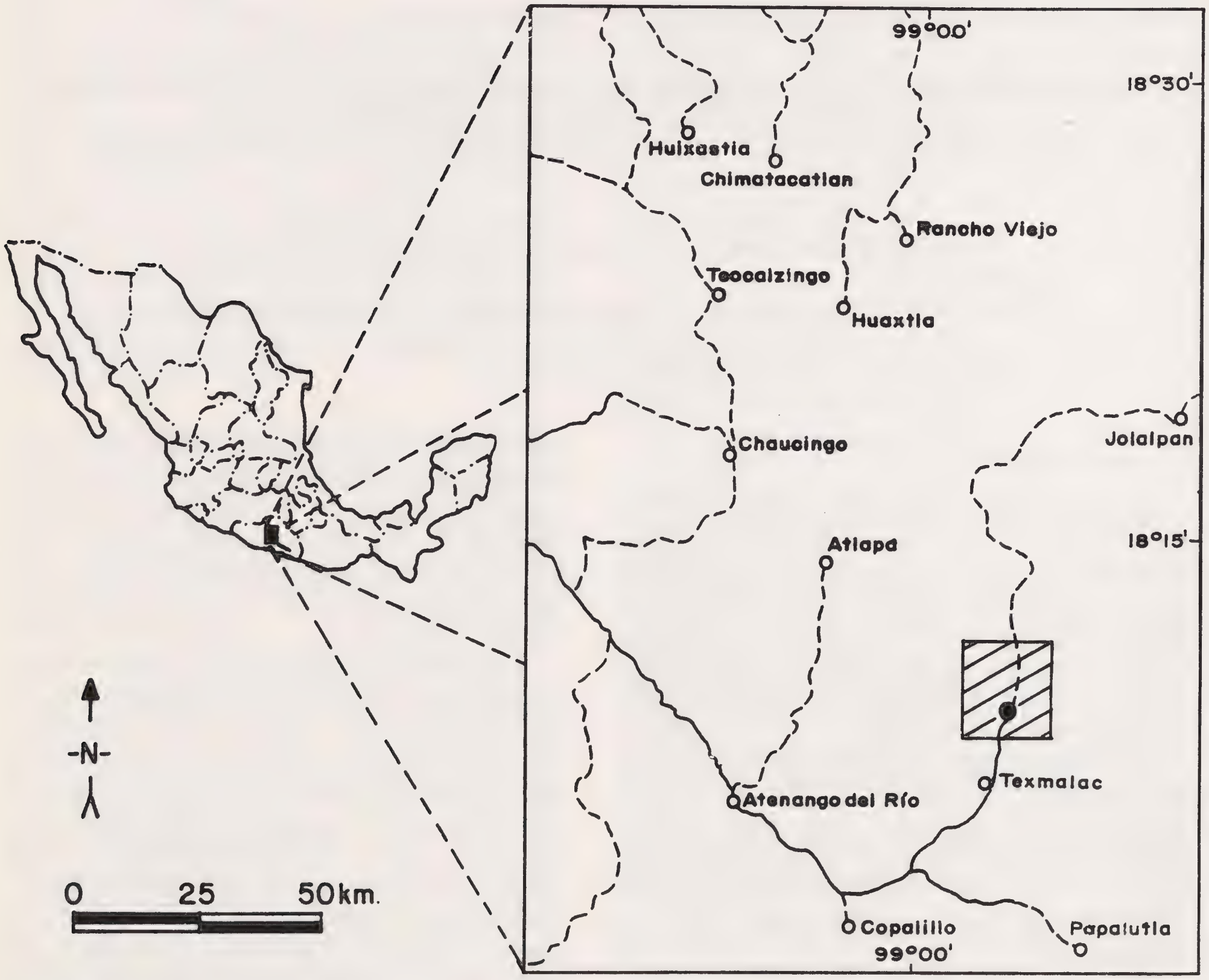

Figure 1. Location map of the studied area (framed) at outcrops from the Mexcala Formation near Texmalac, Guerrero.

mouthensis, Globigerinelloides prairiehillensis, Heterohelix globulosa, and *Pseudotextularia nuttalli.* These species are indicative of a lower Maastrichtian age (Brian Huber, pers. comm.).

Alencáster (1980) suggested a close relationship between the Texmalac fauna and the faunas of the Atlantic and Gulf Coastal Plains. Preliminary systematic studies on certain gastropods and bivalves from Texmalac (Salceda *et al.*, 1995; Vega and Perrilliat, 1995; Vega *et al.*, 1995) suggest paleobiogeographic affinities with the Atlantic and Gulf Coastal Plains, but also with the Caribbean and Tethyan Provinces. More than 25 species of gastropods and 10 species of bivalves have been identified, However, among the gastropods there are some specimens which seem to belong to new genera and new species. Among these, the new species described herein represents one of the most abundant gastropods, including nearly all sizes from juveniles to adults, the latter recognized by the development of a callus that covers the spire completely.

III. SYSTEMATIC PALEONTOLOGY

Phylum MOLLUSCA Linnaeus, 1758
Class GASTROPODA Cuvier, 1797
Subclass PROSOBRANCHIA
Milne-Edwards, 1848
Order MESOGASTROPODA Thiele, 1925
Family STROMBIDAE Rafinesque, 1815
Genus CALYPTRAPHORUS Conrad, 1857

Calyptraphorus CONRAD, 1857, Acad. Nat. Sci. Philadelphia, Proc., v. 9, p. 166.

Type species: Rostellaria velata Conrad, 1833, by subsequent designation, Cossmann, 1904. Eocene; Claiborne, Alabama.

CALYPTRAPHORUS BINODIFERUS
Perrilliat and Vega, n. sp.
Plate 1, figures 1-8
Plate 2, figures 1-8

Description: Shell medium-sized. Protoconch with three, rounded smooth whorls; teleoconch with seven rounded whorls. Sculpture of shell consisting of numerous axial ribs; first whorl with 30 axial, rounded, prosocline ribs; interspaces as wide as ribs. On next whorls ribs lessen, on one whorl 14, on the next 12, with interspaces wider than ribs. On last whorl ribs disappearing, with shell practically smooth. Weak spiral ribs present on spire, being more pronounced near suture. Suture impressed. Aperture not preserved in any specimen. Callus covering entire surface of shell. Canal extending upward, forming a curved channel through the callus, not covering first three whorls of spire; then curving downward. Callus irregularly thickened on either side of groove. The most distinctive feature of the species being the presence of two nodes on the body whorl, one near aperture and another near the canal. No sculpture on the side of body whorl opposite the nodes, with exception of spiral striae near suture.

Holotype: IGM 5887, height 32.5 mm, diameter 17.4 mm.

Paratype: IGM 5888, height 29.2 mm, diameter 19.8 mm.

Type locality: IGM 2448; 125 km south of México City, near the borderline between the states of Puebla, Morelos, and Guerrero. Access from México City is via Highway 95, México-Acapulco. About 5 km beyond Iguala, Guerrero, a crossroad leads to Atenango del Río. From this point, a dirt road to the northeast passes beside Texmalac. About 5.5 km beyond Texmalac, a roadcut on the left side exposes bright brown marls, with a diverse molluscan fauna. The locality is registered in the Locality Catalogus of the Museo de Paleontología of the Instituto de Geología, at the Universidad Nacional Autonóma de México (UNAM).

Occurrence: Mexcala Formation. México; lower Maastrichtian.

Etymology: The name of the species is based on the presence of two nodes on the last whorl.

Discussion: The Mexican specimens have no similarities to any species that have been described from the Upper Cretaceous elsewhere. *Rostellaria palliata* Forbes (1846, p. 129, pl. 13, fig. 15), from the Cretaceous of Pondicherry, India, has a shell that, when full grown, becomes enveloped by the callus, which envelops it so that only the body whorl and part of the first three volutions are exposed. The surface is smooth and polished. Stoliczka (1868, p. 34, pl. 2, figs. 18-20) recorded this species from the Trichinopoly and Arrialoor Groups (Maastrichtian) of South India. These specimens are more inflated, and they have neither tubercles, nor nodes, nor axial ribs.

Rostellaria palliata Forbes also has been reported from the Maastrichtian and Danian from Tunisia, North Africa (Pervinquière, 1912, p. 30, pl. 2, figs. 12-16); from the Senonian of Madagascar as *Rostellaria (Calyptraphorus) palliata* Forbes (Cottreau, 1922, p. 161, pl. 15, figs. 16-19); and from the Upper Cretaceous of Madagascar (Basse, 1932, p. 168, 1933, pl. 10, figs. 11-13) as *Rostellaria (Cyclomolops) palliata* Forbes.

From the Maastrichtian of Jamaica, Trechmann (1927, p. 39, pl. 4, fig. 29) described *Rostellaria (Calyptraphorus)* sp., on the basis of an incomplete specimen, with only some badly preserved whorls of the spire but the callus may be seen. It does not show sculpture. Sohl (1987, p. 1101) also mentioned a new species of *Calyptraphorus* from the Maastrichtian of Ducketts Crossroads Area of Jamaica, without any description.

Our material differs from *Calyptraphorus hopkinsi* Olsson (1934, p. 68, pl. 10, fig. 2; 1944, p. 96, pl. 15, figs. 8, 12) from the Monte Grande Formation (Upper Cretaceous) in Monte Grande, northwestern Peru. These specimens are not wholly covered by the callus. The first whorls of the spire have axial ribs that disappear and the surface of the whorl becomes smooth. The body whorl does not develop nodes.

From the Gramame Formation, Pernambuco, Brasil, Muñiz (1993, p. 128, pl. 11, figs. 5, 8) described *Calyptraphorus*

itamaracensis, of supposed Campanian age, which would be the most ancient species of this genus. The sculpture consists of axially curved opistocyrt ribs, present on the first whorls. This species does not possess tubercules or nodes on the body whorl, differing in this respect from the Mexican specimens.

From the Paleocene and Eocene there are several species of this genus. Specimens of *Calyptraphorus septentrionalis* Stanton (1920, p. 39, pl. 7, figs. 5a-5d, 6), from the Cannonball Marine Member, Lance Formation at Cannonball River, North and South Dakota, have spiral striae and curved ribs, which are obsolete on the last whorls in immature specimens. In mature specimens, a thick callus completely covers the frontal side of the spire, and a thin deposit is found at the dorsal side.

From the lower Eocene there are several species that should be mentioned because they present similarities with the Mexican specimens. *Calyptraphorus trinodiferus* Conrad (1857, p. 166), from the Eocene of Alabama, presents a peculiar accumulation of the callus as three irregular nodes. The middle one is the largest and is formed in the central part of the back of the shell. The other two nodes occur at the beginning and ending of the posterior canal. The Mexican specimens have only two nodes. They differ from *Calyptraphorus indicus* Cossmann and Pissarro (1909, p. 44, pl. 5; figs. 1, 2; pl. 8, figs. 3, 3a) and *Calyptraphorus hollandi* Cossmann and Pissarro (1909, p. 45, pl. 4, fig. 20) from the Eocene of India, neither of which has nodes.

From the Eocene of Maria Farinha, Province of Pernambuco, Brazil, *Calyptraphorus? chelonites* (White, 1887, p. 174, pl. 11, figs. 17-19), has small shells lacking nodes and the number of whorls is indistinguishable.

The differences between our material and *Calyptraphorus velatus nodovelatus* Palmer (1937, p. 243, pl. 32, figs. 1-3, 5, 9), from the Eocene of Alabama, are that this species presents more nodes, and a medium, irregular node near the beginning of the posterior canal, such as in *C. trinodiferus*; an elongated node occurs in the opposite side near the canal's terminus. Callus swellings of irregular size occur also on opposite sides of the body whorl. Examples of *C. jacksoni* Clark (1896, p. 68, pl. 12, figs. 2a, 2b), from the Paleocene of Aquia Creek, Maryland, lack nodes on the body whorl, and are larger than the specimens from Guerrero.

From the Paleocene and Eocene of Nuevo León and Tamaulipas in northeastern México, Gardner described *Calyptraphorus popenoe* (Gardner, 1945, p. 166) from the Midway Formation, in Agualeguas and Cerralvo, Nuevo León, and *Calyptraphorus carrizensis* (*ibid.*, p. 167, pl. 17, figs. 11, 18, 21; pl. 27, fig. 6) from the Eocene Carrizo Sandstone of Alamo River, Tamaulipas-Nuevo León; this species is characterized by its small size, relatively slender outline, and flattened aperture. Paredes-Mejía (1989, p. 191-195) mentioned the presence of two new species of *Calyptraphorus (Calyptraphorus)* (spp. A and B) from the Paleocene Bateque Formation, Baja California. These species are different from the material here described, by being bigger in size, lacking nodes and having four to five whorls.

IV. PALEOBIOGEOGRAPHY AND EVOLUTION

As stated above, Upper Cretaceous

PLATE 1

Figures

1-8. *Calyptraphorus binodiferus* Perrilliat and Vega, n. sp.
- 1,2. (X 1.8) IGM 5887 (holotype); height 32.5 mm, diameter 17.4 mm.
- 3. (X 2.05) IGM 5888 (paratype); height 29.2 mm, diameter 19.8 mm.
- 4,5. (X 1.8) IGM 5889 (paratype); height 33.4 mm, diameter 22.1 mm.
- 6,7. (X 2.65) IGM 5890 (paratype); height 21.9 mm, diameter 11.9 mm.
- 8. (X 2.4) IGM 5891 (paratype); height 25.3 mm, diameter 11.7 mm.

Locality of all: IGM 2448, Mexcala Formation, Guerrero, México.

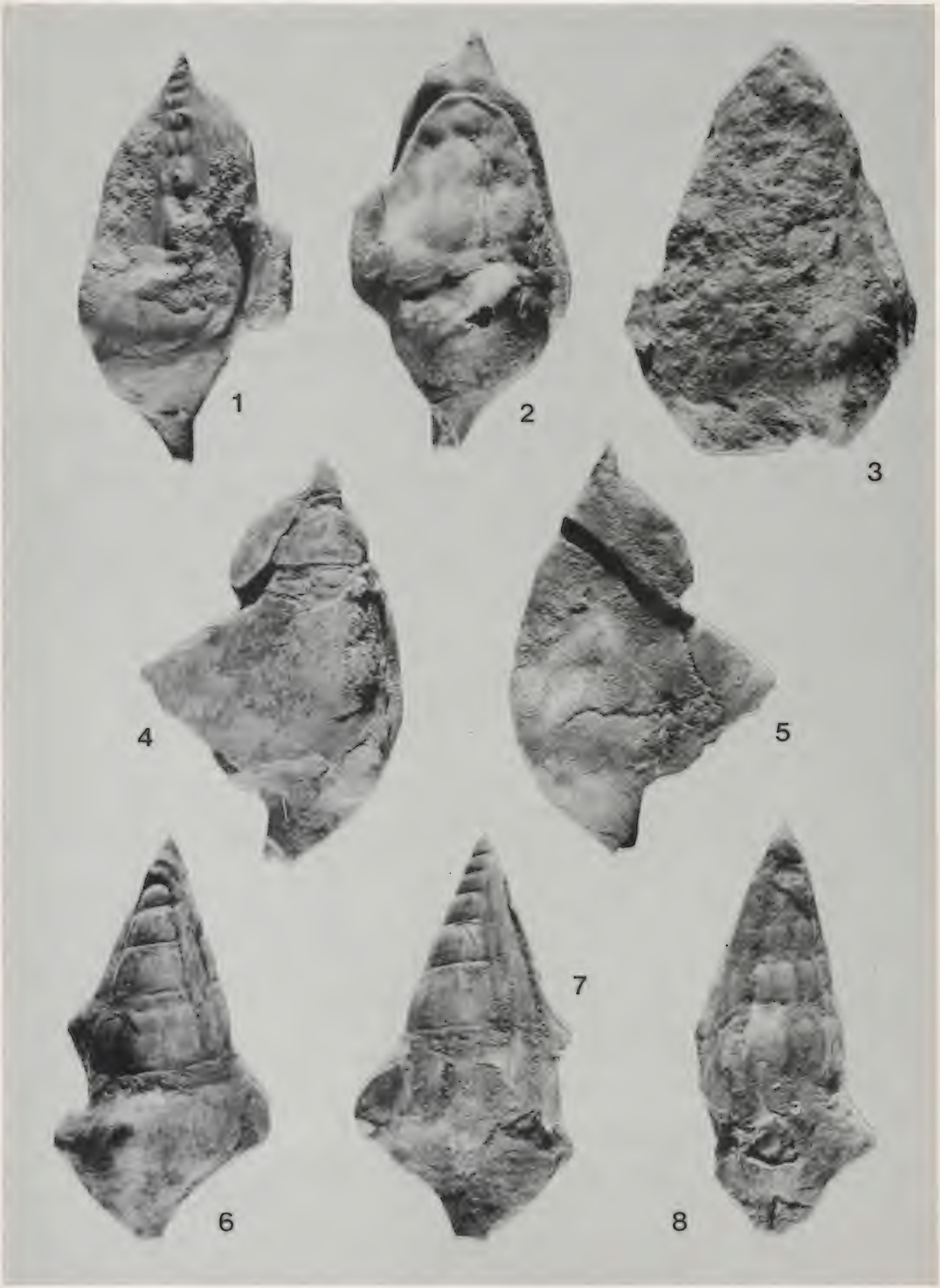

PLATE 1

species of *Calyptraphorus* have been reported from Jamaica, Peru, Brazil, Tunisia, Madagascar, and India. The oldest species is *C. itamaracensis* from the Campanian of Brazil. No species from the Upper Cretaceous possess nodes on the body whorl, except for *C. binodiferus* n. sp. The other species of this genus, which do show nodes are *C. trinodiferus* and *C. velatus nodovelatus*, both from the Eocene of Alabama. Considering development of nodes as an evolutionary trend into a phyletic line of *Calyptraphorus*, it seems reasonable to propose that *C. binodiferous* is the ancestral species, which gave rise to the nodose Eocene species (Fig. 2).

It is evident that during the Late Cretaceous, *Calyptraphorus* had a wide distribution, all around the Tethyan Province. Although during early Tertiary time some species prevailed in this province (*Rostellaria palliata*, Paleocene of Tunisia; *Calyptraphorus indicus* and *C. hollandi*, Eocene of India; *Calyptraphorus? chelonites*, Eocene of Brazil), there was an expansion of the distribution northward in North America, to the Pacific realm (*Calyptraphorus* spp. A and B, Paleocene of Baja California), the Western Interior (*C. septentrionalis*, Paleocene of North and South Dakota), and to the Atlantic and Gulf Coastal Plains (*C. jacksoni*, Paleocene of Maryland; *C. popenoe*, Paleocene of northeastern México; *C. carrizensis*, Eocene of northeastern México; *C. trinodiferus, C. velatus,* and *C. velatus nodovelatus*, Middle Eocene of Alabama; *C. stamineus*, Late Eocene of Louisiana and Mississippi). Along with this northward migration, there was an increase in size and of amount covered by the callus, as compared with the size and morphology between Cretaceous and Tertiary species.

Figure 2 summarizes paleobiogeographic distribution and possible phyletic relationships between Cretaceous and Tertiary species of *Calyptraphorus*. It seems important to note that genus-level survivorship across the K-T boundary and northward migration to the Pacific realm and Gulf Coast Plain also has been registered for crustacean genera such as *Lophoranina*, which also had a Tethyan distribution during Late Cretaceous, and migrated during early Tertiary to Baja California, Alabama, Europe, the Middle East, and the Indo-Pacific, becoming extinct by Oligocene time (Feldmann *et al.*, 1996). There are more groups like these to be restudied and reevaluated in terms of paleobiogeographic, biostratigraphic and evolutionary implications. Most gastropods at the studied area show strong spines and/or nodes. This feature could be related to a high predation pressure, mainly by crustaceans and other gastropods. It seems important to continue searching for poorly known Maastrichtian and early Tertiary faunas.

V. ACKNOWLEDGMENTS

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PLATE 2

Figures

1-8. *Calyptraphorus binodiferus* Perrilliat and Vega, n. sp.
- 1,2. (X 2.5) IGM 5892 (paratype); height 24.1 mm, diameter 12.7 mm.
- 3. (X 3.0) IGM 5893 (paratype); height 20.5 mm, diameter 9.9 mm.
- 4. (X 3.3) IGM 5894 (paratype); height 18.5 mm, diameter 8.7 mm.
- 5. (X 2.06) IGM 5895 (paratype); height 29.6 mm, diameter 14.7 mm.
- 6. (X 2.4) IGM 5896 (paratype); height 25.4 mm, diameter 13.2 mm.
- 7,8. (X 2.5) IGM 5897 (paratype); height 23.7 mm, diameter 12.4 mm.

Locality of all: IGM 2448, Mexcala Formation, Guerrero, México.

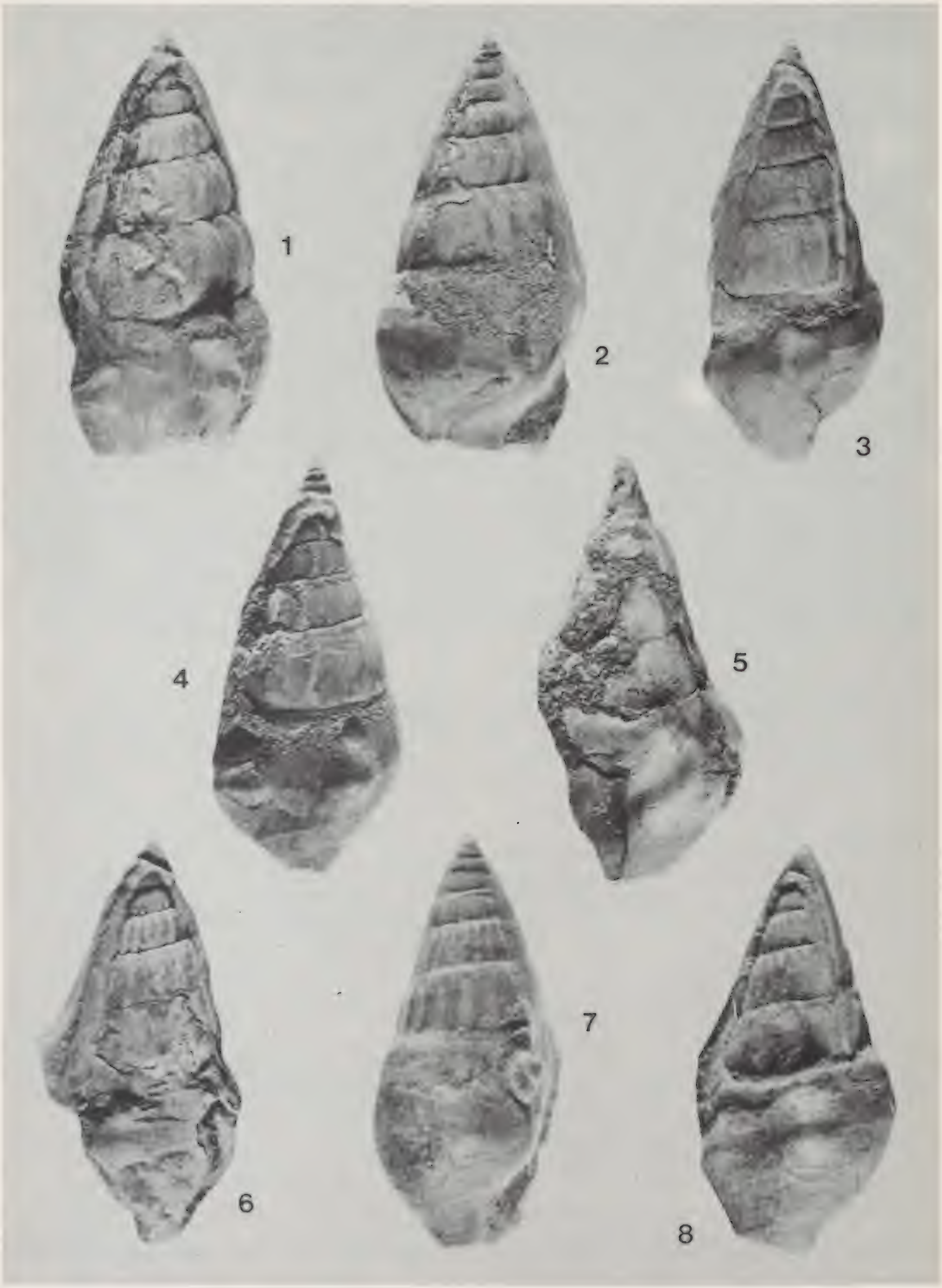

PLATE 2

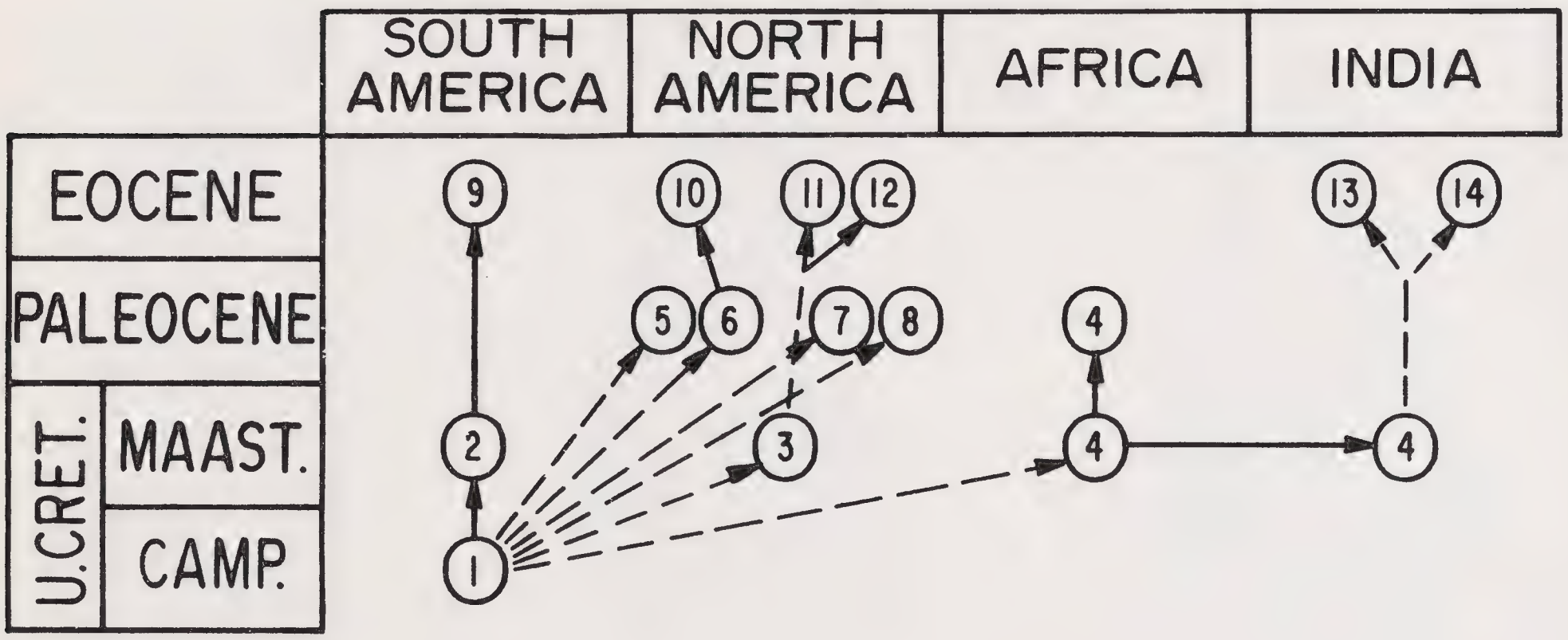

Figure 2. Paleobiogeographic and evolutionary table for species of *Calyptraphorus* from Late Cretaceous to early Tertiary. 1, *C. itamaracensis* (Campanian, Brazil); 2, *C. hopkinsi* (Maastrichtian, Peru); 3, *C. binodiferus* (Maastrichtian, México); 4, *Rostellaria palliata* (Maastrichtian, Madagascar; Maastrichtian and Paleocene, Tunisia); 5, *Calyptraphorus* spp. (Paleocene, Baja California, México); 6, *C. popenoe* (Paleocene, Nuevo León, México), 7, *C. septentrionalis* (Paleocene, North and South Dakota); 8, *C. jacksoni* (Paleocene, Alabama), 9, *Calyptraphorus? chelonites* (Eocene, Brazil); 10, *C. carrizensis* (Eocene, Tamaulipas, México); 11, *C. trinodiferus* (Eocene, Alabama); 12, *C. velatus nodovelatus* (Eocene, Alabama); 13, *C. indicus* (Eocene, India); 14, *C. hollandi* (Eocene, India).

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THE GENUS *LEUCOZONIA* (GASTROPODA: FASCIOLARIIDAE) IN THE NEOGENE OF TROPICAL AMERICA

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ABSTRACT

The fasciolariid neogastropod genus *Leucozonia* Gray, 1847, is represented in the Neogene of tropical America by four species: *L. ocellata* (Gmelin, 1791) from the Mare Formation (Late Pliocene) of Venezuela, not treated here; *L. nassa* (Gmelin, 1791), of which *L. caribbean*a Weisbord, 1962, from the Playa Grande Formation (Pleistocene) of Venezuela is a synonym; *L. rhomboidea* (Gabb, 1873) from the Gurabo Formation (Early Pliocene) of the Dominican Republic; and *L. striatula*, n. sp., from the Cercado and lower Gurabo formations (Late Miocene to Early Pliocene) of the Dominican Republic. *Leucozonia rhomboidea* closely resembles the Recent *L. leucozonalis* (Lamarck, 1822) from the northwestern Caribbean and an unnamed Recent species from the Brazilian island of Fernando de Noronha. *Leucozonia striatula* is very similar to the Recent *L. brasiliana* (d'Orbigny, 1841) from the Atlantic coasts of Central and South America.

INTRODUCTION

Species of the fasciolariid neogastropod genus *Leucozonia* are common inhabitants of low rocky intertidal and sublittoral communities in tropical America and the Cape Verde Islands. Despite its ecological prominence, *Leucozonia* is poorly represented in the fossil record. Only two fossil species, *L. rhomboidea* (Gabb, 1873) from the Neogene of the Dominican Republic and *L. caribbeana* Weisbord, 1962, from the Mare Formation (Late Pliocene) of Venezuela have been described. A third species, the Recent *L. ocellata* (Gmelin, 1791), has been recognized in the Mare Formation (Gibson-Smith and Gibson-Smith, 1979), and will not be discussed further here. In this paper, I critically assess the fossil species, and describe *L. striatula*, n. sp., from the Late Miocene and Early Pliocene of the Dominican Republic.

ABBREVIATIONS

ANSP - Academy of Natural Science, Philadelphia, Pennsylvania
NMB - Naturhistorisches Museum, Basel, Switzerland
USNM - United States Museum of Natural History, Washington, D. C.
PRI - Paleontological Research Institute, Ithaca, New York

SYSTEMATICS

Family FASCIOLARIIDAE Gray, 1853
Subfamily PERISTERNIINAE Tryon, 1880
Genus LEUCOZONIA Gray, 1847

Leucozonia GRAY, 1847, Zoological Society of London, Proceedings, v. 15, p. 184.

Type species: *Murex nassa* Gmelin, 1791, by monotypy.

Remarks: Bullock (1974) and Lyons (1991) have pointed out that *Latirus gibbulus* (Linnaeus, 1758), the Indo-West Pacific type species of *Latirus* Montfort, 1810, is very similar in the character of its radula and shell to *Leucozonia*, and that *Leucozonia* may therefore be a junior subjective synonym of *Latirus*. Woodring (1928) recognized that *Latirus* is a heterogeneous group requiring thorough revision, especially among its Indo-West Pacific species. Lyons (1991) referred many fossil and Recent species from the Americas to *Latirus*, but remarked that none of these belong to *Latirus* in the strict sense, as typified by L. *gibbulus*. I have chosen to retain *Leucozonia* as a valid genus, pending a thorough revision of *Latirus* and of such related taxa as *Ascolatirus* Bellardi, 1884; *Dolicholatirus* Bellardi, 1884; *Fractolatirus* Iredale, 1936; *Fusolatirus* Kuroda and Habe *in* Kuroda *et al.*, 1971; *Glaphyrina* Finlay, 1927; *Hemipolygona* Rovereto, 1899 (*Latirus* group 1 of Lyons, 1991); *Hesperisternia* Gardner, 1944; *Latirolagena* Harris, 1897; *Latirulus* Cossmann, 1889; *Neolatirus*

Bellardi, 1884; *Nodopelagia* Hedley, 1915; *Opeatostoma* Berry, 1958; *Peristernia* Mörch, 1852; *Polygona* Schumacher, 1817 (*Latirus* group 2 of Lyons, 1991); *Pseudolatirus* Bellardi, 1884; *Taron* Hutton, 1883; and *Teralatirus* Coomans, 1965.

Leucozonia is characterized by a relatively short, broadly open anterior siphonal canal, by three or four basal columellar folds, a well-marked parietal rib at the adapical end of the inner lip, by having the inner side of the outer lip sculptured by granulated lirae, and usually by having a labral tooth at the outer lip situated at the end of a prominent spiral cord. Below this cord, the last whorl is constricted; that is, it has a concave lateral profile. At least two species, *L. cerata* (Wood, 1828) from the tropical eastern Pacific and *L. ocellata* (Gmelin, 1791) from the tropical western Atlantic, differ from typical *Leucozonia* by having the lirae on the inner side of the outer lip smooth, by having the outer lip planar instead of convex when viewed from the apertural side, and by lacking the labral tooth. The species discussed below all belong to the more typical group of *Leucozonia*.

LEUCOZONIA NASSA (Gmelin, 1791)

Leucozonia caribbeana WEISBORD, 1962, Bulletins of American Paleontology, v. 42, no. 193, p. 361-362, pl. 32, figs. 9, 10.

Remarks: Weisbord (1962) named *Leucozonia caribbeana* from the Maiquetia Member of the Playa Grande Formation of Venezuela. Gibson-Smith and Gibson-Smith (1979) argued that this unit is continuous with, and part of, the Mare Formation, to which they assign a Middle or Late Pliocene age. Gonzalez de Juana *et al.* (1980) regarded the Maiquetia Member as a distinct unit and considered it to be of Pleistocene age. The great majority of species in both the Maiquetia Member and the Mare Formation are still living in Venezuelan waters (Gibson-Smith and Gibson-Smith, 1979). I suspect both units represent the Early Pleistocene.

Weisbord (1962) distinguished *L. caribbeana* from *L. nassa* because the fossil has seven instead of nine shoulder knobs, three instead of four columellar folds, and a wider, more oblique, anterior siphonal canal. The holotype of *L. caribbeana* (PRI 26261) is an immature shell in which the inner side of the outer lip is smooth instead of being ornamented with granulated lirae. Like typical *L. nassa* from the insular Caribbean Recent fauna, *L. caribbeana* has prominent shoulder knobs, three closely spaced spiral cords on the upper part of the last whorl, and a well-developed labral tooth at the end of a fourth primary cord, which is separated from the three upper cords by a spirally threaded sector. Recent *L. nassa* is variable in the number and prominence of shoulder knobs and in the number of columellar folds. The shoulder always forms the widest part of the shell, and bears seven to ten knobs. These knobs are formed where the shoulder cord is crossed by strong axial ribs, whose lower end is marked by the tooth-bearing cord. Recent specimens have three to four (rarely five) columellar folds. I have seen Recent *L. nassa* from Florida, the Bahamas, Saint Maarten, Guadeloupe, Curaçao, and the Brazilian island of Fernando de Noronha. Given the variation observed in Recent *L. nassa*, I see no basis for separating *L. caribbeana*, and I therefore consider *L. caribbeana* as a junior subjective synonym of *L. nassa*.

LEUCOZONIA STRIATULA, new species
Figures 1, 2

Diagnosis: Leucozonia with well-developed axial ribs, fine spiral threads, a distinct labral tooth, and a long anterior siphonal canal.

Description: Shell moderately large, maximum height 49.1 mm, fusiform, diameter 52-61% of shell height; spire moderately low, last whorl comprising 65-68% of total shell height; protoconch consisting of one smooth whorl; teleoconch consisting of five whorls separated by indistinct, appressed suture; last whorl with angulate shoulder above at widest part of shell, constricted at base; shoulder becoming rounded on last quarter of whorl of large specimens; spiral sculpture of last whorl consisting of ten fine cords on concave subsutural ramp, nine to twelve low cords between shoulder and tooth-bearing cord, and ten to twelve fine cords below tooth-bearing cord; axial sculpture consisting of eight to eleven low, broad, rounded ribs, extend-

ing from suture to suture in spire whorls, and from suture to tooth-bearing cord on last whorl; axial ribs weak and irregular on last quarter whorl of large specimens; outer lip sharp, crenulated at edge, medially convex when viewed from apertural side; sharp labral tooth formed at end of prominent spiral cord at abapical end of convexly rounded sector of last whorl; outer lip forms broad, shallow, concave sinus below labral tooth on abaxial side of siphonal canal; inner side of outer lip with ten deeply recessed lirae; inner lip adherent, with three basal columellar folds; well-developed parietal rib at adapical end of inner lip in large specimens; aperture elongate-ovate, its height:breadth ratio 2.7-2.9; anterior siphonal canal long, 33-40% of total apertural height; siphonal fasciole low, rounded; umbilicus absent.

Holotype: USNM 490523; height 38.5 mm, maximum diameter 22.7 mm, height of aperture plus canal 25.2 mm, breadth of aperture 9.3 mm.

Paratype 1: NMB H 17804, height 49.1 mm, maximum diameter 30.0 mm.

Figures 1, 2: *Leucozonia striatula*, new species. USNM 490523 (holotype), height 38.5 mm; locality TU 1422.
Figures 3, 4: *Leucozonia rhomboidea* (Gabb, 1873). USNM 490550, height 35.4 mm; locality TU 1354.

Paratype 2: ANSP 79634; height 44.0 mm, maximum diameter 24.7 mm.

Paratype 3: PRI 44387; height 41.9 mm, maximum diameter 22.6 mm.

Type locality (holotype and paratypes 1 and 2): locality TU 1422, Arroyo Bellaco, Cercado Formation, Dominican Republic.

Other localities: Paratype 3, locality TU 1215, lower Gurabo Formation, Río Gurabo, bluffs above ford on Los Quemados-Sabaneta Road, Dominican Republic.

Other material examined: Three specimens, locality TU 1422; five specimens, locality TU 1215.

Stratigraphic and geographic distribution: Cercado Formation (Late Miocene) and lower Gurabo Formation (Early Pliocene), Dominican Republic.

Remarks: In several characters, *Leucozonia striatula* represents an intermediate condition between species of *Polygona* (*Latirus* group 2 of Lyons, 1991) and typical *Leucozonia*. Like species of *Polygona*, the new species has a relatively long anterior siphonal canal and fine spiral sculpture. In most species of *Polygona*, spiral sculpture is not as fine as in *L. striatula*, but the number of cords on the last whorl is low as in *L. nassa, L. ocellata*, the deep-water western Atlantic *L. jacarusoi* Petuch, 1987, the eastern Atlantic (Cape Verde Islands) *L. triserialis* (Lamarck, 1822), or the eastern Pacific *L. cerata* (Wood, 1828), *L. rudis* (Reeve, 1846), and *L. tuberculata* (Broderip, 1833). *Leucozonia striatula* differs from tropical American members of the genus *Polygona* by having a distinct labral tooth at the end of a cord, which marks the abapical end of the axial sculpture.

The species most similar to *L. striatula* is the Recent western Atlantic *L. brasiliana* (d'Orbigny, 1841), which is distributed on the coasts of Central and South America, south to southern Brazil. *Leucozonia striatula* differs from *L. brasiliana* by having a slightly lower spire (last whorl comprising 65-68% instead of 63-64% of total shell height), generally fewer axial ribs (eight to eleven as compared to ten to thirteen in *L. brasiliana*), by having the widest part of the shell at the shoulder instead of below the shoulder, and by having finer spiral threads between the shoulder and the suture. *L. brasiliana* was considered to be a synonym of *L. nassa* by Marcus and Marcus (1962). Both *L. brasiliana* and *L. striatula* differ from *L. nassa*, however, in having about ten fine cords between the shoulder and the tooth-bearing cord. In *L. nassa*, there are three large cords at and just below the shoulder, separated from the tooth-bearing cord by fine threads. Most specimens of *L. nassa*, moreover, are less slender than *L. brasiliana* and *L. striatula* (diameter 57-69% as compared to 52-61% of total shell height).

Like *L. rhomboidea* (below), *L. striatula* is found in reef facies (see Saunders *et al.*, 1986). The living *L. brasiliana* occurs in similar habitats.

Leucozonia rhomboidea (Gabb, 1873)
Figures 3, 4

Lagena rhomboidea GABB, 1873, American Philosophical Society, Transactions, new ser., v. 15, p. 218.

Leucozonia rhomboidea (Gabb). PILSBRY, 1922, Proceedings of the Academy of Natural Sciences of Philadelphia, v. 73, p. 345, pl. 21, fig. 9.

Description: Shell medium-sized, maximum height 39.7 mm, fusiform; diameter 62-65% of total shell height; spire moderately low, last whorl comprising 61-65% of total shell height; protoconch consisting of one smooth whorl; teleoconch consisting of six whorls separated by adpressed, indistinct suture; last whorl without shoulder, evenly rounded above, weakly constricted at base; spiral sculpture of penultimate whorl consisting of about sixteen fine threads; spiral sculpture of last whorl consisting of about ten weak basal cords, and of about twenty-three very fine threads on upper part of whorl; axial sculpture consisting of about ten low, rounded ribs on spire whorls, absent on all or least half of last whorl; outer lip medially convex when viewed from apertural side, with labral tooth at end of uppermost spiral cord; inner side of outer lip with eleven lirae; inner lip adherent, with three basal columellar folds; parietal rib situated at adapical end of inner lip in larger specimens; aperture elongate-ovate, its height: breadth ratio 2.5-2.7; anterior siphonal canal 27-31% of total apertural height; siphonal fasciole rounded; umbilicus absent.

Material examined: ANSP 2947 (lectotype),

Cibao region, Dominican Republic; ANSP 79165 (paralectotype), Cibao region, Dominican Republic; NMB locality 16818, Cañada de Zamba, Dominican Republic; USNM 490550, Cañada de Zamba, locality TU 1354, Dominican Republic (figs. 3, 4).

Stratigraphic and geographic distribution: Gurabo Formation (Early Pliocene), Cañada de Zamba, Dominican Republic.

Remarks: Dall (1890, p. 106) thought that Gabb's *Lagena rhomboidea* might be a young specimen belonging to the genus *Mazzalina* Conrad, 1860, but Pilsbry (1922, p. 345) correctly recognized it as a *Leucozonia*. The species closely resembles the Recent *L. leucozonalis* (Lamarck, 1822) from the northwestern Caribbean. Both species reach the same maximum height of about 40 mm. They have a rounded, finely spirally threaded last whorl, and lack a distinct shoulder. *Leucozonia leucozonalis* is generally somewhat more slender (diameter 53-65% of total shell height), lacks the axial sculpture of the upper whorls of *L. rhomboidea*, and has a slightly longer canal (33-36% instead of 27-31% of total apertural height).

An even more similar form is an unnamed Recent species from Fernando de Noronha that previous authors have considered a variety of *L. nassa* (see Smith, 1890; Lopes and Alvarenga, 1955; Matthews and Kempf, 1970; Leal, 1991). This Recent species differs from *L. rhomboidea* by having a somewhat broader shell (diameter 68-74% instead of 62-65% of shell height), a relatively shorter siphonal canal (17-21% instead of 27-31% of apertural length), and in having ten low, rounded, broad, obsolete axial ribs on the last whorl instead of having the last whorl partly or entirely devoid of axial ribs.

The two previously known specimens of *L. rhomboidea* (ANSP 2947 and 79165) are immature shells with a height of about 10 mm. One of these (ANSP 2947, the lectotype) is the only specimen with the protoconch preserved. New material shows that the species attains a height of at least 39.7 mm, a height comparable to that of other species of *Leucozonia*.

Leucozonia rhomboidea has been collected at a single locality, TU 1354 (= locality NMB 16818), in the Early Pliocene part of the Gurabo Formation. The assemblage at this locality represents a coral community of the kind in which *L. leucozonalis* commonly lives today (see Saunders *et al.*, 1986; Vermeij, 1973).

Two of five specimens of *L. rhomboidea* from TU 1354 bear eroded pits evidently excavated by a hipponicid gastropod. I shall report on these pits and their makers in a separate paper.

DISCUSSION

Its Late Miocene occurrence makes *L. striatula* the oldest known member of the genus *Leucozonia*. Further collecting in older deposits will probably reveal even earlier representatives. The available evidence shows that a labral tooth evolved in *Leucozonia* no later than the Late Miocene. Many other gastropods also evolved a labral tooth during the Miocene in tropical America. These include members of the muricid subfamilies Muricinae, Ocenebrinae, and Rapaninae. Species of Pseudolividae and the olivid subfamily Ancillinae inherited the labral tooth from Paleogene ancestors. Oddly enough, the large muricid fauna of the Miocene and Pliocene of the Dominican Republic (Vokes, 1989) is highly unusual among Neogene tropical American muricid assemblages in lacking species with a labral tooth. Pseudolivids and ancillines are also absent from the Late Neogene Dominican fauna. Did the evolution of a labral tooth in *Leucozonia* in the reef environments of the Dominican Republic fill an adaptive gap left vacant by other groups? Further work on the biogeography and phylogeny of gastropods with a labral tooth may shed further light on this interesting possibility.

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NASSARIUS (MOLLUSCA:NEOGASTROPODA) FROM THE NEOGENE OF NORTHWESTERN ECUADOR

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ABSTRACT

The nassarid fauna from the Neogene formations of northwestern Ecuador consists of five species, none of which are known from either the Recent or fossil faunas of the Caribbean or Pacific. There is one species with affinities to the western Pacific Recent fauna, one with affinities to Recent species in both the Caribbean and eastern Pacific faunas, the remaining three species are known only from the Ecuadorian Neogene, one of which, *Nassarius mcmakini*, n. sp., is confined to the Angostura Formation.

INTRODUCTION

It is generally accepted that there was free passage of water between the Caribbean Sea and the Pacific Ocean, through the Isthmus of Panamá, for much of the Tertiary Period, allowing exchange of molluscan species. It has been suggested that the closure took place about 3.5 MA (Saito,1976). Jones and Hasson (1985) accepted this date as the most likely time when migration of species ended, with final emergence of the Isthmus at about 3 MA or later.

The Neogene faunas of northwestern Ecuador have either direct or indirect relationship to Caribbean or Pacific faunas, both Recent and fossil. This paper will discuss nassarid species from two Neogene formations of northwestern Ecuador, ranging in age from Late Miocene to Late Pliocene, and their relationship to Caribbean and Pacific faunas. It is not intended to be a monograph of the Family Nassariidae.

The five species discussed in this paper are all endemic to the Neogene of northwestern Ecuador. One species, *N. mcmakini*, n. sp., from the Angostura Formation has affinities with species in the Recent East Pacific, as well as the Caribbean Recent and fossil faunas. *Nassarius mastus* Olsson, 1964, was described from the Picaderos Formation, and occurs in both the Angostura and Onzole formations. Other species include: *N. thielei* Olsson, 1964, from the Esmeraldas beds, with affinities to an Indo-Pacific species; *N. hylus* Olsson, 1964, known only from the the Esmeraldas beds; and one species *N. repetiti* Olsson, 1964, known only from the Onzole Formation.

The Angostura Formation of Late Miocene age (planktic foraminiferal zone N. 16) is the oldest formation discussed in this paper. The name was first published by Stainforth (1948, pp. 142, 143, 146) following an unpublished report of the International Ecuadorian Petroleum Company (*fide* Bristow and Hoffstetter, 1977, p. 32).

The name "Esmeraldas Formation" was proposed by Olsson (1942, p. 260) for the highly foraminiferal tuffaceous shales exposed along the coast of Esmeraldas Province and the Esmeraldas River. Bristow and Hoffstetter (1977, p. 143) recognized the name Esmeraldas Formation but considered it to be part of the Onzole Formation. Vokes (1988, p. 4) found it difficult to accept the name Onzole Formation for the mollusk-rich deposits along the Esmeraldas coast from Punta Gorda to Camarones and used the term "Esmeraldas beds" for these deposits exposed at the top of the Onzole Formation.

Olsson (1964, p. 10), in discussing fossils from the Picaderos Formation, stated that the name came from the village of Picaderos, which is near the center of the outcrop on the Río Santiago. He listed 16 species of mollusks from the Picaderos Formation. Of these five occur at Picaderos, four occur at Playa de Tigre, three are not mentioned in the text, two only occur at Cueva de Angostura (Angostura Formation), one is from Playa de Tigre and Picaderos, and one is in the text but not on the faunal list.

Olsson described the Picaderos Formation as occurring along the Río Santiago near the village of Picaderos; however, in the text he shows two

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Picaderos species as occurring along the Río Onzole and considerd some Picaderos species as being from the Borbon Formation.

Bristow and Hoffstetter (1977, p. 219, 232) state that the name Picaderos Formation is in disuse and consider it to be equal to the Onzole Formation. The Servicio Nacional de Geología y Minera (Cuadro no. 83) also considers the Picaderos Formation to be equal to the Onzole Formation; however, it places Olsson's Playa de Tigre locality at the border of the Onzole and Angostura formations and within the Angostura Formation. Olsson's collecting data is not precise enough to know exactly how close to Playa de Tigre he made his collections, thus it is difficult to know in which formation this locality should be placed. Olsson, in the text, also listed some species as occurring at Picaderos; Borbon Formation. It is possible that some of his collecting data is in error and we may never know where some of his specimens were really collected.

ABBREVIATIONS FOR REPOSITORY INSTITUTIONS

CASG - California Academy of Sciences, San Francisco, California.
USNM - United States National Museum of Natural History, Washington D.C.
PRI - Paleontological Research Institution, Ithaca, New York.

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SYSTEMATIC PALEONTOLOGY

Phylum MOLLUSCA Cuvier, 1797
Class GASTROPODA Cuvier, 1797
Subclass PROSOBRANCHIA
Milne-Edwards, 1848
Superorder CAENOGASTROPODA
Cox, 1959
Order NEOGASTROPODA Thiele, 1925
Superfamily MURICOIDEA
Rafinesque, 1815
Family NASSARIIDAE Iredale, 1916
Subfamily NASSARIINAE

Genus NASSARIUS Dumeril, 1806

Nassarius DUMERIL, 1806, Zool. Anal., p. 166.
Type species: Buccinum arcularia Linn., 1758, by monotypy.

Subgenus NASSARIUS s.s.
NASSARIUS (NASSARIUS) REPETITI
Olsson
Plate 1, figure 4

Nassarius repetiti OLSSON, 1964, Neogene Moll. Northwest. Ecuador, p. 146, pl. 24, figs. 6, 6a.

Description: "The shell is small, subovate, with an elevated sharp spire of about seven whorls, including that of the small nucleus consisting of one turn. The sculpture of the spire whorls consists of three rows of sharply beaded spiral cords which stand high above the adjacent sutural zones, which thus appear as if deeply excavated, the fine suture itself lying away in the bottom as if hidden. The spirals on the apertural side of the body whorl number about seven with an additional eight or nine, much smaller ones, partly smooth lying along the basal sulcus and over the short beak in front. The spiral cords are neatly beaded by small axials which faintly undulate the spiral interspaces. On mature specimens, the sculpture is obsolete on the back of the body whorl, replaced there by a large smooth patch. The aperture is broadly subovate with a short longitudinal posterior canal at its junction with the parietal wall. The outer lip is thickened by a rib on the back, and bears on its inner side four or more small denticles. There is a thin spread of callus over the inner lip through which the underlying spiral cords still show through; the parietal callus extends downward over the pillar is a small shelflike feature *[sic]*, bearing four small denticles along it. The siphonal canal notch is deep, its sides a little elevated, its fasciole marked with small smooth spirals but has no bordering keel." (Olsson, 1964)

Holotype: USNM 643999; height 14.6 mm, diameter 7.8 mm.

Type locality: Onzole Formation, Telembi, Esmeraldas Prov., Ecuador.

Occurrence: Onzole Formation, Ecuador.

Discussion: Nassarius repetiti is similar to *N. complanatus* (Powys, 1835) from the Tropical East Pacific but differs in being larger, more slender with the spire whorls slightly convex rather than straight sided. Olsson (1964, p. 145) placed Telembi in the Angostura Formation; however, Bristow and Hoffstetter (1977, p. 218) place the locality at Telembi within the Onzole Formation.

NASSARIUS (NASSARIUS) MCMAKINI
Pitt and Pitt, n. sp.
Plate 1, figure 1

Description: Shell small; five whorls, plus a protoconch of about two rounded, smooth whorls, end broken. First spire whorl expanding abruptly, axial sculpture appearing immediatly, but eroded on early whorls; remaining spire whorls with eleven axial ribs crossed by about six spiral grooves (both specimens worn). Suture distinct. Body whorl large with nine strong, retractive axial ribs from suture to base, crossed by numerous, spiral, rounded grooves, interspace of equal width. First axial posterior to aperture with signs of numerous spiral bands; however, shell too worn to determine number or extent. Apertural callus pad heavy, covering all of shell face; outer lip thickened. Anterior canal narrow, recurved. Outer lip with about six lirations with short secondary lirations between.

Etymology: This new species is named for Allan McMakin from Astoria, Oregon, who has done most of the photography for this and past papers.

Holotype: CASG 67832.01; height 8.0 mm, diameter 5.1 mm.

Paratype: PRI 44212; height 8.7 mm, diameter 5.9 mm.

Type locality: P-103, Angostura Formation, sea cliffs about 300 meters west of Punta Verde, about 2 1/4 km east of the mouth of Río Verde and about 22 km east of the bridge over Río Esmeraldas, Esmeraldas Prov., Ecuador.

Occurrence: Angostura Formation, Ecuador.

Discussion: Nassarius mcmakini, n. sp., may be compared to the Tropical East Pacific species *N. iodes* (Dall, 1919), *N. moestus* (Hinds, 1844), and *N. tiarula* (Kiener, 1841), which occurs as far north as San Francisco, California [as *N. tegula* (Reeve, 1853), see Skoglund, 1992, p. 85]. *Nassarius iodes* differs from *N. mcmakini* in having three or four weak lirations on the inner side of the outer lip and one much larger one posterior to the others at about the center of the aperture. The body whorl of *N. iodes* has ten axial ribs, fading out on the last one-third of the whorl, which are crossed by seven spiral grooves; the columellar callus pad is thin. *Nassarius moestus* differs in having four short lirations on the inner side of the outer lip and one much larger than the rest, posterior to the others at the center of the aperture. In *N. moestus* the body whorl has ten beaded, axial ribs with smooth interspaces, fading out on the last one-third of the whorl. *Nassarius tiarula* differs in having five short lirations on the inner side of the outer lip with one much larger liration posterior to the rest, at the center of the aperture. The Plio-Pleistocene and Recent western Atlantic and Caribbean species *N. vibex* (Say, 1822), differs in having four lirations on the inner side of the outer lip and one much larger liration posterior to the rest, at the center of the aperture. The body whorl has nine axial ribs, crossed by twelve spiral bands, not fading out on the last one-third of the whorl, and the columellar callus is not well developed.

Subgenus PROFUNDINASSA Thiele, 1929

Profundinassa THIELE, 1929, Handbuch der Systematische Weichtierkunde, pt. 1, p. 323.

Type species: Nassarius babylonicus Watson, 1882, by monotypy.

NASSARIUS (PROFUNDINASSA) THIELEI
Olsson
Plate 1, figures 5,6

Nassarius (Profundinassa) thielei OLSSON, 1964, Neogene Moll. Northwest. Ecuador, p. 145, pl. 24, fig. 7.

Description: "Shell small, subovate, the spire twice the height of the aperture. The nucleus is relatively large, turbinate, with two or three smooth convex whorls. Postnuclear whorls,

about four, are shouldered around the upper third, the angle of which carries a strong cord. The body whorl is large and forms about a half the whole shell, quadrate in shape, widest about the middle, the base strongly contracted. The sculpture is formed by about eight axial riblets which are noded by the shoulder cord and by flat closeset spiral threads which cover the surface between the shoulder angle and the beak. The space above the shoulder angle is essentially smooth, except for small spirals. Aperture subovate, with a calloused shelf on the parietal wall, the outer lip thin, smooth within. There is a short, nassoid beak formed by the contraction around the base. End of columellar pillar with a sharp keel which margins the siphonal canal notch. Siphonal fasciole strong, bordered by a nassoid keel." (Olsson, 1964)

Holotype: USNM 644190; height 14.1 mm, diameter 7.2 mm.

Type locality: Esmeraldas beds, Punta Gorda, Esmeraldas Prov., Ecuador.

Occurrence: Esmeraldas beds, Ecuador.

Discussion: In comparing our specimens of *N. thielei* to specimens from Olsson, 1964, we find *N. thielei* to be a quite variable species. Our specimens from Punta Gorda (fig. 6), mostly incomplete and worn, have the shoulder angle from almost turreted to moderately angled, the shoulder cord is almost non-existant in some specimens. The axial ribs vary from vertical in the figured specimen to protractive. The spiral threads are weak in our specimens, although this appears to be due to wear. The whorls on the figured specimen are straight sided, although on some of the fragmentary specimens they are more rounded. If we had more specimens this could possibly prove to be an undescribed species.

This common species, as noted by Olsson, is similar to *N. babylonica* Watson, 1882, from the Philippine Islands but has a single cord at the shoulder rather than a double cord and the protoconch whorls are not carinate. *Nassarius babylonica* occurs in the Recent western Pacific and Indian Oceans.

Subgenus UZITA H. Adams and A. Adams, 1853

Uzita H. ADAMS and A. ADAMS, 1853, The genera of Recent Mollusca, v. 1, p. 120.

Type species: Buccinum miga Bruguière, 1789, by subsequent designation, Cossmann, 1901.

NASSARIUS (UZITA) HYLUS Olsson

Plate 1, figure 2

Nassarius (Uzita) hylus OLSSON, 1964, Neogene Moll. Northwest. Ecuador, p. 145, pl. 37, figs. 10, 11.

Description: "Shell small, subovate, stout, the spire about twice the aperture and composed of about six whorls. The nuclear whorls are large, with a turbinate coil of two and one-half to three rapidly enlarging smooth turns developing a small keel and a few axials near the end. The sculpture consists of low, narrow, axial riblets (12 to 14) crossed by alternating spiral threads producing a coarse cancellation. The aperture is subovate, rimmed with a narrow, nearly continuous, calloused peristome, finely denticulated on both lips. Beak short, encircled by a fasciolar fold." (Olsson, 1964)

Holotype: USNM 644000; height 10.5 mm, diameter 5.8 mm.

Type locality: Esmeraldas beds, Quebrada Camarones, Esmeraldas Prov., Ecuador.

Occurrence: Esmeraldas beds, Ecuador.

Discussion: Nassarius exsarsus (Dall, 1908), a deep water species from the Galápagos Islands, is similar in outline; however, the spire whorls are turreted, the axial and spiral sculpture is closer together and more subdued.

NASSARIUS (UZITA) MASTUS Olsson

Plate 1, figure 3

Nassarius (Uzita) mastus OLSSON, 1964, Neogene Moll. Northwest. Ecuador, p. 146, pl. 38, fig. 7.

Description: "The shell is small, stout, pupoid, its protoconch unusually large for its size, the nuclear stage followed by a single, sculptured turn (that of the body whorl). The large protoconch is composed of four, smooth convex whorls, the first small, the others enlarging rapidly to form a turbinate coil. The nuclear stage is followed by the sculptured body whorl. Assumption of the adult sculpture is gradual with the appearance of a few widely spaced axial lines intersected by two or three spiral

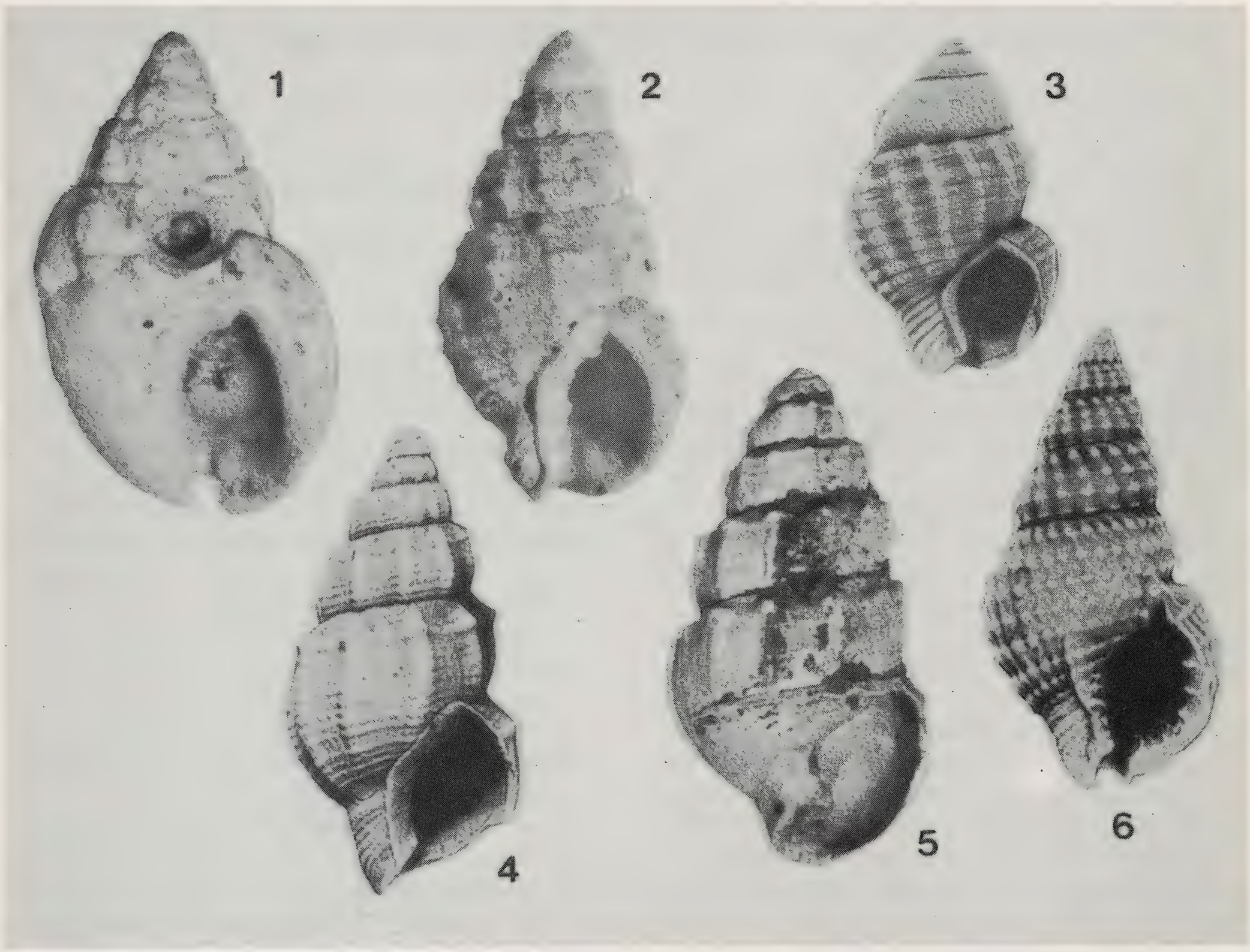

PLATE 1

Figures

1. *Nassarius (Nassarius) mcmakini* Pitt and Pitt, n. sp. 137
   CASG 67832.01 (holotype); height 8.0 mm, diameter 5.1 mm (X6.5).
   Locality: P-103, Angostura Formation.
2. *Nassarius (Uzita) hylus* Olsson, 1964 138
   CASG 67833.01; height 11.1 mm, diameter 5.9 mm (X4.5).
   Locality: P-100, Onzole Formation, Ecuador.
3. *Nassarius (Uzita) mastus* Olsson, 1964 138
   USNM 644194 (holotype); after Olsson, pl. 38, fig. 7); height 2.9 mm, diameter 1.8 mm (X12.1).
   Locality: Onzole Formation, Ecuador.
4. *Nassarius (Nassarius) repetiti* Olsson, 1964 136
   USNM 645278 (paratype, after Olsson, pl. 24, fig. 6); height 13.5 mm, diameter 6.4 mm (X3.6).
   Locality: Onzole Formation, Ecuador.
5. *Nassarius (Profundinassa) thielei* Olsson, 1964 137
   USNM 644190 (holotype; after Olsson, pl. 24, fig. 7a); height 14.1 mm, diameter 7.2 mm (X3.4).
   Locality: Onzole Formation, Ecuador.
6. *Nassarius (Profundinassa) thielei* Olsson, 1964 137
   CASG 67834.01; height 12.0 mm, diameter 5.9 mm (X4.4).
   Locality: P-99, Onzole Formation, Ecuador.

Page

threads, the axials number about 12 and the spirals finally to eight or nine, their points of intersection forming small nodes on the final portion of the whorl. The base is narrowly constricted a little above the short beaked anterior canal, but there is no definite fasciole or a nassoid keel. The outer lip is thickened and a little reflected, marked with lirations within. Columellar area is deeply excavated, smooth, the end of the pillar with a small plait." (Olsson, 1964)

Holotype: USNM 644194, height 2.9 mm, diameter 1.8 mm (not found).

Type locality: Onzole Formation, Picaderos, Esmeraldas Prov., Ecuador.

Occurrence: Angostura and Onzole formations, Ecuador.

Discussion: Olsson (1964, p. 146) noted that this species has a large protoconch and only one post-nuclear whorl, which gives the appearance of an immature shell; however, this single whorl is sculptured and the outer lip is thickened and lirate within as would be expected in an adult shell. We have no explanation for this condition unless, as happens in some Recent Tropical East Pacific species, after the eggs are laid, the adults leave the area. The juveniles could have been covered by some natural condition and fossilized with no adults present.

We have not been able to locate the holotype at USNM. There are two vials containing numerous specimens, one marked "Picaderos" and the other "various localities."

LOCALITY DATA

The following are Pitt fossil collecting localities:

P-99. Esmeraldas beds, Punta Gorda (intertidal), about 8 km west of Las Palmas, Esmeraldas Prov., Ecuador.

P-100. Esmeraldas beds, east bank of Estero Camarones, east of the village of Camarones, about 10 km east of the mouth of Río Esmeraldas, Esmeraldas Prov., Ecuador.

P-103. Angostura Fm., sea cliffs about 300 meters west of Punta Verde, about 2 1/4 km east of the mouth of Rió Verde and about 22 km east of the bridge over Rió Esmeraldas, Esmeraldas Prov., Ecuador.

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TWO NEW GASTROPODS FROM THE PLIOCENE PINECREST BEDS OF FLORIDA

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New species continue to be discovered from the mollusk-rich Pliocene Pinecrest Beds near Sarasota, Florida. Two new gastropods are described herein, each of which is a large-sized member of a genus not commonly found in the fossil record. The first, a *Morum*, appears to be an intermediate species between the Miocene *M. chipolanum* and the Recent *M. dennisoni*. The second, apparently a *Phenacovolva*, is perhaps the only representative of that genus, fossil or Recent, in the Western Atlantic. Both are known only from single specimens.

SYSTEMATIC PALEONTOLOGY

Class GASTROPODA
Family HARPIDAE Bronn, 1849
Subfamily MORUMINAE Hughes and Emerson, 1987
Genus MORUM Röding, 1798

Morum RÖDING, 1798, Museum Boltenianum, pt. 2, p. 53.

Type species: *Morum purpureum* Röding, 1798 [= *Strombus oniscus* Linnaeus, 1767], by monotypy.

Subgenus ONISCIDIA Mörch, 1852

Oniscidia MÖRCH, 1852, Catalogus Conchyliorum ... Comes de Yoldi, pt. 1, p. 111.

Type species: *Oniscidia cancellata* Sowerby, 1824, by monotypy.

MORUM (ONISCIDIA) MEGANAE
Raymond, n. sp.
Plate 1, figure 1

Description: Shell triangularly ovate, large for genus, the single known specimen measuring 61 mm in height with protoconch missing; five postnuclear whorls; shoulder ramp initially flat, giving a stepped appearance to spire, but becoming more sloped on body whorl; spire ornamentation of 14 axial ribs crossed initially by one, and finally two, low flattened spiral cords on penultimate whorl; body whorl strongly cancellate, with 12 prominent spinose axial ribs and 12 strong, flattened spiral cords forming short, blade-like hooked spines at each juncture with axial ribs; intervarical areas with one weak spiral thread just below major cord, and numerous fine axial growth lamellae, giving a linen-like texture to intervarical area; aperture elongate, strong posterior notch, large parietal shield flaring to top of penultimate whorl; well-defined sulcus at posterior commisure; parietal shield covered with variously sized pustules (up to 1 mm in diameter) and short (less than 3 mm) linear lirations; pattern of shield ornamentation distinctly lineate, paralleling underlying revolving cords, but also noticeable along underlying axial ribs; outer lip thickened, recurved abaperturally, covered by 35-40 fine lirae of varying lengths; siphonal canal slightly recurved dorsally.

Holotype: UF 70001; height 61.0 mm, diameter 41.4 mm.

Type locality: UF SO017; Pinecrest Beds, APAC pit, 4 miles east of Sarasota, Florida (E 1/2 Sec.12, T36S, R18E, Bee Ridge Quadrangle, U.S.G.S. 7.5' series).

Etymology: This species is named for the author's daughter, Megan, who, at the age of five weeks, was probably the youngest visitor ever to the Sarasota APAC Pit.

Discussion: This shell is similar to *Morum dennisoni* (Reeve, 1842) in both size and appearance, but is somewhat broader with a less sloping shoulder. The ornamentation of the parietal shield of *M. dennisoni* is also different, consisting of fine pustules, which in some specimens tend to be lineate adaperturally. The holotype of *M. dennisoni* Reeve (1842, pl. 253, figs. 5,6) discussed at length in Dance and Emerson (1967), is similar to *M. meganae* except for the above mentioned characteristic.

Comparisons to fossil specimens of *M. chipolanum* (Maury, 1925), *M. obrienae* (Olsson and Petit, 1964), and *M. macgintyi* (Smith, 1937), and to specimens of the Recent *M. dennisoni* at the Florida Museum of Natural History, were made by the author. Among the fossil species, *Morum meganae* most closely resembles *M. chipolanum*, sharing its low spire and sharply shouldered outline. *Morum chipolanum* also has a parietal shield that reflects the underlying sculpture. The pustules for *M. chipolanum* are coarser and

generally more elongate, and the outer lip of *M. chipolanum* has about half as many lirae as *M. meganae. Morum chipolanum* also lacks a well-defined sulcus at the posterior commisure. Typical specimens of *M. chipolanum* measure about 32 mm.

Morum macgintyi (= M. obrienae) is a smaller shell with coarser and more elongate pustules ornamenting the parietal shield, fewer lirae, and only about eight revolving cords. *Morum domingense,* which has also been considered a fossil analogue of *M. dennisoni*, has a slightly higher spire and a more sloped shoulder. It also differs from *M. meganae* in the parietal shield ornamentation, which in *M. domingense* is made up of randomly placed pustules only slightly elongated in an adapertural direction, and the number of lirae on the outer lip, which number 24-30. *Morum domingense* reaches at least 38 mm. The Recent *M. lindae* (Petuch, 1987) has 16 axial ribs, and its parietal shield ornamentation is similar to *M. dennisoni*.

Morum meganae was found in spoil from the west-central portion of the south end of the APAC pit, slightly south of where the separator was located. It is very probable that the shell is from unit 7 (Petuch, 1982). Other material collected at the same time contained no shells marking units below 7. There is always a remote possibility that it came from a higher unit. The shell was found in 1983 by the author. Regrettably, APAC (known previously as the MacAsphalt, Newburn, or Warren Brothers pit), is now flooded.

The rareness of *M. meganae* is perhaps due to its probable habitat of deeper water (over 30 meters), assuming it lived as *M. dennisoni* does. This would place it on the border of the deepest water thought to have covered the Pinecrest beds (Allmon, 1993).

Lastly, the size of *M. meganae* is most remarkable, especially when one considers that the other fossil Western Atlantic species have heights which are about half that of *M. meganae*. The listed record for *M. dennisoni* is 64 mm, virtually equal to the *M. meganae* specimen if the missing protoconch is considered.

Family OVULIDAE Fleming, 1828

Genus PHENACOVOLVA Iredale, 1930

Phenacovolva IREDALE 1930, Mem. Qld. Mus., v. 10, no. 2, p. 85.

Type species: *Phenacovolva nectarea* Iredale, 1930, by original designation.

PHENACOVOLVA MARYPALMERAE Raymond, n. sp.

Plate 1, figure 2

Description: Shell large for the genus, the single known specimen measuring over 50 mm in height; elongate fusiform, ventricose, convolute, equally attenuate and subacuminate at both ends; spire concealed; aperture narrowly crescent-shaped, longitudinal, slightly wider near anterior end, notched anteriorly and posteriorly; outer lip smooth, inflexed, slightly thickened, forming a somewhat flattened arc of about 70 degrees; body whorl smooth, with maximum diameter and depth slightly towards posterior end. No funiculum, fossula or carinal ridge apparent. Very slight swelling near posterior notch, possibly indicating obsolete funiculum.

Holotype: UF 75000; height 53.4 mm, diameter 12.2 mm.

Type locality: UF SO013; Pinecrest Beds, Quality Aggregates, Inc. pit, 5 miles east of Sarasota, Florida (Sec.7/8, T36S, R19E, Bee Ridge Quadrangle, U.S.G.S. 7.5' series).

Etymology: This shell is named for Mary Palmer of Alva, Florida, a long time avid fossil collector.

Discussion: The assignment of this shell to the genus *Phenacovolva* must be considered tentative, and will raise eyebrows of others besides the author. According to Cate (1973), the genus primarily inhabits the Pacific Ocean, with a few species found in the Indian Ocean and *P. piragua* (Dall, 1889) possibly the only species in the Caribbean. *Phenacovolva piragua* was originally considered a *Simnia* by Dall (1889), a *Neosimnia* by Schilder (1932), and again a *Simnia* by Abbott (1974). It has not previously been reported from the Florida fossil record. However, the similar genus *Simnialena* does appear (Petuch, 1994).

The last major systematic revision of Ovulidae was done by Cate (1973), who based his work on Schilder and Schilder (1971). Considerable ambiguity remains among the distinguishing characteristics of several similar genera. A key characteristic is the presence or absence of a funiculum. It is present in *Simnialena* Cate, 1973, *Subsimnia* Cate, 1973, and

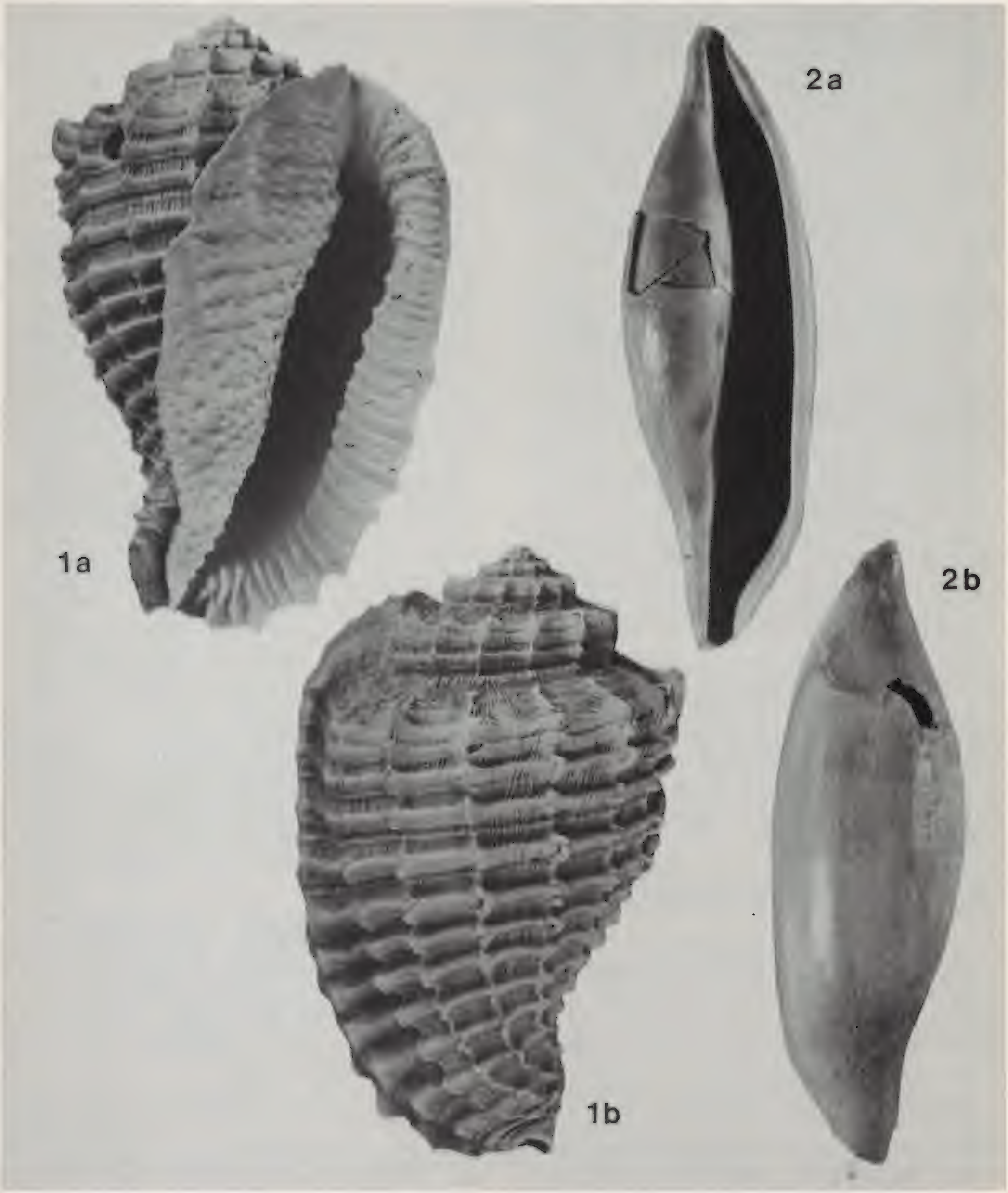

PLATE 1

1. *Morum meganae* Raymond, n. sp. (x 1-1/4)
   UF 70001 (holotype); height 61.0 mm, diameter 41.4 mm.
   Locality: UF SO017, Sarasota, Florida; Pinecrest beds.
2. *Phenacovolva marypalmerae* Raymond, n. sp. (x 1-1/2)
   UF 75000 (holotype); height 53.4 mm, diameter 12.2 mm.
   Locality: UF SO013, Sarasota, Florida; Pinecrest beds.

Neosimnia Fischer, 1884, but may or may not be present in *Simnia* Risso, 1826, and *Phenacovolva*. *Delonovolva* Cate, 1973, does not mention a funiculum, although it is present in all species of *Delonovolva* he lists, as well as in all species of *Simnia* he lists.

Phenacovolva is a rather widely varying genus, and allows all of the characteristics shown by *P. marypalmerae*, which has neither a funiculum nor a carinal ridge, although the faint swelling near the posterior end may be the vestige of a funiculum. Additionally, *Phenacovolva* is known to include several species larger than 50 mm, while other similar genera rarely exceed 25 mm.

There are few comparisons to be made to other species in the fossil record. Petuch (1994, plate 33, figures L, P and S) illustrates three examples of *Simnialena*, of which *S. donovanae* from the Pinecrest Beds is closest in overall form. Its holotype (13 mm) has both a funiculum and fossula, as does *S. digelae* (17 mm).

Phenacovolva marypalmerae was found in 1995 in spoil at phase six of the Quality Aggregates, Inc. pit (also known as Richardson Road shell pit and Wendell Kent pit). The anonymous finder believes it is most likely from unit 10, although material from units 7 through 11 was exposed at the time.

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NEW SPECIES OF CANCELLARIOIDEA (MOLLUSCA:GASTROPODA) FROM THE LOWER MIOCENE CANTAURE FORMATION OF VENEZUELA

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INTRODUCTION

The neogastropod superfamily Cancellarioidea is well represented in the Cantaure Formation, exposed in a series of arroyos about 500 meters south of "Casa Cantaure," 14 km west of Pueblo Nuevo, Paraguaná Peninsula, Falcón, Venezuela. Eight species of the superfamily were reported and figured by Jung (1965), two of which are here described as new. Three additional new species and one previously unrecorded from the Cantaure Formation, collected by one of us (BML) on two field trips in 1992 and 1995, brings the total number of Cancellariidae known from the Cantaure Formation to twelve. These are placed in eight genus-group taxa, of which three are previously unreported from this formation (Table 1). With the exceptions of *Cancellaria (Charcolleria) terryi* Olsson, 1942, described from the Pliocene Charco Azul beds of Panama and later recorded from the Pliocene Esmeraldas beds of Ecuador (Olsson, 1964, p. 124) and *Narona barystoma* Woodring, 1970, described from the Pliocene Gatun Formation of Panama, the other ten species are endemic to the Miocene of Venezuela.

SYSTEMATIC PALEONTOLOGY

Class GASTROPODA

Superfamily CANCELLARIOIDEA

Family CANCELLARIIDAE Forbes and Hanley, 1851

Genus CANCELLARIA Lamarck

Cancellaria LAMARCK, 1799, Soc. Hist. Nat. Paris, Mem. 1, p. 71.

Type species: *Voluta reticulata* Linné, 1767, by monotypy.

Subgenus CANCELLARIA sensu stricto

CANCELLARIA (CANCELLARIA) HODSONAE Landau and Petit, n. sp.

Cancellaria (Cancellaria) aff. *rowelli* Dall. JUNG, 1965, Bulls. Amer. Paleontology, v. 49, no. 223, p. 551, pl. 75, figs. 7, 8.

Description: Protoconch smooth, of about three volutions. Teleoconch of about five whorls. Sculpture beginning with rather strong axials soon crossed by four or five spiral cords weaker than ribs. On body whorl some axial ribs thickened like varices. On teleoconch whorls two spiral cords at shoulder more prominent. Suture impressed. Outer lip thickened, with about eight lirae within. Siphonal fasciole well-developed, rounded and forming a small umbilicus partially covered by a thin columellar callus. Columella with three folds, adapical one largest and abapical one forming edge of short, slightly recurved siphonal canal.

Holotype: Naturhistorisches Museum Basel H 13761; height 21.3 mm, diameter 10.5 mm (Jung, 1965, pl. 75, fig. 7).

Type locality: NMB 17516, Cantaure Formation; series of arroyos about 500 meters south of "Casa Cantaure," which is 14 km (by road) west of Pueblo Nuevo, Paraguaná Peninsula, Falcón, Venezuela.

Paratype: Naturhistorisches Museum Basel H 13762; height 19.3 mm, diameter 10.2 mm (Jung, 1965, pl. 75, fig. 8). Locality NMB 17516, Cantaure Formation, Paraguaná Peninsula, Falcón, Venezuela.

Etymology: Named for Helen King Hodson, in recognition of her work on the Cantaure Formation.

Discussion: This species was fully described and discussed by Jung (1965, p. 551). He compared *Cancellaria* aff. *rowelli* with *C. rowelli* Dall, 1896, from the Baitoa Formation of the Dominican Republic, but pointed out consistent differences between the two. Jung and Petit (1990, p. 99) also did not accept the Cantaure specimens as being *C. rowelli*. *Cancellaria hodsonae* is smaller and proportionally narrower than

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C. rowelli and has much stronger sculpture at the shoulders formed by very heavy spiral cords. The opportunity to study additional specimens from both Venezuela and the Dominican Republic has convinced us that the two species are distinct.

Subgenus BIVETIELLA Wenz

Bivetiella WENZ, 1943, Handbuch der Paläozoologie, v. 6, Gastropoda, pt. 6, p. 1356.

Type species: *Cancellaria similis* Sowerby, 1833, by original designation.

CANCELLARIA (BIVETIELLA) JUNGI Landau and Petit, n. sp.

Cancellaria (Cancellaria) epistomifera Guppy. JUNG, 1965, Bulls. Amer. Paleontology, v. 49, no. 223, p. 548, pl. 75, figs. 1, 2. Not of Guppy, 1876.

Description: Protoconch smooth, of about two and one-half volutions. Postnuclear whorls about six in number. Sculpture beginning with weak spiral cords soon crossed by heavier axial ribs. On later whorls spiral cords and axial ribs about equal in strength. Varices developed as teleoconch increases in size, usually with three per whorl. On body whorl a few secondary spiral cords appearing in interspaces between primary cords. Suture very deep for subgenus. Outer lip prosocline, slightly everted at stromboid notch, with about a dozen lirae within. Parietal callus weak. Columella with three folds, center one sometimes slightly bifurcate, anterior one forming edge of recurved siphonal canal.

Holotype: Naturhistorisches Museum Basel H 13757; height 30.1 mm, diameter 18.4 mm (Jung, 1965, pl. 75, figs. 1, 2).

Type locality: NMB 17516, Cantaure Formation; series of arroyos about 500 meters south of "Casa Cantaure," which is 14 km (by road) west of Pueblo Nuevo, Paraguaná Peninsula, Falcón, Venezuela.

Etymology: Named for Peter Jung of Basel, Switzerland, in recognition of his work on the Cantaure Formation.

Discussion: This species was fully described by Jung (1965, p. 548-550), who had only one adult specimen and nine juveniles. In his remarks, Jung mentioned that the Cantaure specimens differed from the Dominican Republic specimens of *Cancellaria epistomifera* Guppy, 1876, which have more inflated body whorls, less conspicuous varices, no secondary spirals on the body whorl and a slightly thicker parietal callus. A larger series collected by one of us (BML) confirms that these differences are consistent. Jung and Petit (1990, p. 103) removed Jung's 1965 reference from the synonymy of *C. epistomifera* and placed both *C. epistomifera* and the Venezuelan species in the subgenus *Bivetiella.*

Cancellaria jungi differs from *C. bajonensis* Jung and Petit, 1990, in being more attentuate and possessing less angular features.

Subgenus CHARCOLLERIA Olsson

Charcolleria OLSSON, 1942, Bulls. Amer. Paleontology, v. 27, no. 106, p. 61.

Type species: *Cancellaria (Charcolleria) perdiciana* Olsson, 1942, by original designation.

Table 1. Cancellariidae occurring in the Cantaure Formation, Venezuela.

Cancellaria (Cancellaria) hodsonae, n. sp.
Cancellaria (Cancellaria) lavelana H.K. Hodson, 1931
Cancellaria (Bivetiella) beata Jung, 1965
Cancellaria (Bivetiella) jungi, n. sp.
Cancellaria (Bivetiella) paraguanensis H.K. Hodson, 1931
Cancellaria (Euclia) werenfelsi Jung, 1965
Cancellaria (Charcolleria) terryi Olsson, 1942
Cancellaria (Charcolleria) emilyvokesae, n. sp.
Cancellaria (Massyla) cantaurana, n. sp.
Trigonostoma woodringi Jung, 1965
Axelella yara, n. sp.
Narona barystoma Woodring, 1970

CANCELLARIA (CHARCOLLERIA) EMILYVOKESAE
Landau and Petit, n. sp.
Plate 1, figure 1

Description: Protoconch eroded, of about two volutions. Four teleoconch whorls, well-rounded with deeply impressed suture. Shell fusiform, solid, with a high spire. Body whorl slightly angled at periphery. Spiral sculpture of numerous fine, evenly spaced cords. Axial sculpture consisting of rounded ribs, about 20 in number on penultimate whorl, becoming obsolete on body whorl, being gradually replaced by broad axial folds increasing in strength towards outer lip. Outer lip prosocline, lirate within. Columella with three folds, adapical one largest and extending to edge of weak parietal callus, having behind it a small umbilicus. Oblique anterior fold forming edge of pronounced siphonal canal.

Holotype: Naturhistorisches Museum Basel H 17787; height 26 mm, diameter 18.4 mm (Plate 1, fig. 1).

Type locality: NMB 17516, Cantaure Formation; series of arroyos about 500 meters south of "Casa Cantaure," which is 14 km (by road) west of Pueblo Nuevo, Paraguaná Peninsula, Falcón, Venezuela.

Etymology: Named for Emily H. Vokes of Tulane University, New Orleans, Louisiana, for her help and encouragement.

Discussion: Cancellaria emilyvokesae is closest to *Charcolleria distinguenda* Petit, 1970, from the Chipola Formation of northern Florida but differs from that species in having a sharply angled periphery, weaker and more numerous spiral cords, and more pronounced axial sculpture. Jung (1969, p. 542-543, pl. 58, fig. 3) described, but did not name, a *Cancellaria (Charcolleria)* sp., from the Melajo Clay, Late Miocene of Trinidad. That species is closest to the Late Pliocene *Cancellaria (Massyla) venusta* Tuomey and Holmes, 1856. The distinction between *Massyla* and *Charcolleria* lessens, as our knowledge of the Cancellariidae of the Caribbean area increases.

Subgenus MASSYLA Adams and Adams

Massyla H. ADAMS and A. ADAMS, 1854, Gen. Rec. Moll., v. 1, p. 278.

Type species: *Cancellaria corrugata* Hinds, 1854, by monotypy.

CANCELLARIA (MASSYLA) CANTAURANA
Landau and Petit, n. sp.
Plate 1, figure 2

Description: Protoconch smooth, of about two to two and one-half volutions. Shell small for subgenus. Four well-rounded teleoconch whorls with deeply impressed suture. Body whorl with 14 to 18 irregularly spaced spiral cords, single weaker cord in some interspaces. Axial sculpture of prosocline growth lines and seven to eleven rounded ribs increasing in prominence with age. Outer lip prosocline, strongly and deeply lirate within. Columella vertical, with three folds, adapical one largest and extending to edge of parietal callus, having behind it a small but deep umbilicus. Anterior fold oblique and forming edge of short siphonal canal. Adapical portion of outer lip bearing a weak fold, having within a small, shallow posterior canal.

Holotype: Naturhistorisches Museum Basel H 17788; height 21 mm, diameter 15.5 mm (Plate 1, fig. 2).

Type locality: NMB 17516, Cantaure Formation; series of arroyos about 500 meters south of "Casa Cantaure," which is 14 km (by road) west of Pueblo Nuevo, Paraguaná Peninsula, Falcón, Venezuela.

Unfigured paratype 1: Bernard Landau collection; height 20.5 mm, diameter 13 mm. Locality NMB 17516, Cantaure Formation, Paraguaná Peninsula, Falcón, Venezuela.

Unfigured paratype 2: Bernard Landau collection; height 19 mm, diameter 11.5 mm. Locality NMB 17516, Cantaure Formation, Paraguaná Peninsula, Falcón, Venezuela.

Etymology: Named after the Cantaure Formation.

Discussion: Although this attractive little shell lacks the rapid enlargement in the early growth stages that is characteristic of *Massyla* from later formations, it possesses the other features of the subgenus. This Cantaure species has a more elevated spire than most representatives of the subgenus and has a third very weak columellar fold. It is most similar to *Cancellaria (Massyla) lopezana* Jung and Petit, 1990, from the late Early to early Middle Miocene Baitoa Formation of the Dominican Republic, and *C. (M.) jadesi* Olsson, 1964, from the Late Miocene Angostura Formation of northwestern Ecuador. However, both of those species

have more depressed spires, a greater whorl expansion rate, weaker axial folds on the body whorl and more pronounced constriction behind the siphonal fasciole. This new species is not common in the Cantaure Formation, being known at present from only six specimens (the holotype and five paratypes in the collections of the authors).

Genus AXELELLA Petit

Axelella PETIT, 1988, The Nautilus, v. 102, p. 130.

Type species: *Cancellaria smithii* Dall, 1888, by original designation.

AXELELLA YARA Landau and Petit, n. sp.
Plate 1, figure 3

Description: Protoconch eroded. Teleoconch scalate, large for genus. Whorls rounded, five in number, with spiral sculpture of about eleven primary spiral cords, four or five of these visible on spire whorls, with secondary and tertiary spiral threads in interspaces. Axial sculpture of seven or eight distinct collabral axial ribs on penultimate whorl, decreasing to six or seven on body whorl, the latter becoming narrowly rounded with age. Aperture roughly trigonal, rounded at shoulder. Suture deeply impressed. Outer lip with about twelve interior lirations, not extending to lip, but extending well into aperture. Columella vertical, with three distinct folds, adapical one being largest. Anterior canal shallow and elongated. Inner lip reflected over parietal wall as a thin callus, having behind it a deep umbilicus of variable width, with a tendency in some specimens for final portion of body whorl to become disjunct.

Holotype: Naturhistorisches Museum Basel H 17785; height 25 mm, diameter 13 mm (Plate 1, fig. 3).

Type locality: NMB 17516, Cantaure Formation; series of arroyos about 500 meters south of "Casa Cantaure," which is 14 km (by road) west of Pueblo Nuevo, Paraguaná Peninsula, Falcón, Venezuela.

Unfigured paratype 1: Bernard Landau collection; height 21 mm, diameter 11 mm. Locality NMB 17516, Cantaure Formation, Paraguaná Peninsula, Falcón, Venezuela.

Unfigured paratype 2: Bernard Landau collection; height (incomplete) 21 mm, diameter 12 mm. Locality NMB 17516, Cantaure Formation, Paraguaná Peninsula, Falcón, Venezuela.

Etymology: After Yara, a siren in Amazonian mythology.

Discussion: These Cantaure specimens appear to be closest to two species from the correlative Chipola Formation of northern Florida, *Axelella firma* Petit and Schmelz, 1991, and *A. axiologa* Petit and Schmelz, 1991. The Cantaure species is easily distinguished from the former by its more elongate shape and the presence of an umbilicus. It is more nearly allied to the latter by the presence of an umbilicus and in having similar spiral sculpture but may be differentiated by the greater strength of the columellar folds, the more elongated anterior canal and more marked constriction of the body whorl behind the siphonal fasciole. *Axelella williamsi* (Petit, 1976), from the Pliocene Yorktown Formation of Virginia, has a similar shape but only has two columellar folds and differs in details of sculpture.

Axelella yara is rare in the Cantaure Formation, known only from the holotype and two paratypes.

Genus NARONA Adams and Adams

Narona H. ADAMS and A. ADAMS, 1854, Gen. Rec. Moll., v. 1, p. 277.

Type species: *Cancellaria clavatula* Sowerby, 1832, by subsequent designation (Jousseaume, 1887, Le Naturaliste, Ann. 9, p. 222).

NARONA BARYSTOMA Woodring
Plate 1, figure 4

Cancellaria (Narona) barystoma WOODRING, 1970, U.S. Geol. Survey, Prof. Paper 306-D, p. 342, pl. 53, figs. 5, 6.

Figured specimen: Naturhistorisches Museum Basel H 17786; height 19.5 mm, diameter 10 mm. Locality: NMB 17516, Cantaure Formation; Paraguaná Peninsula, Falcón, Venezuela.

Discussion: The specimen figured by Woodring from the Early Pliocene Gatun Formation of Panama is more elongated, has a stronger posterior columellar fold and has a narrower aperture than specimens from Venezuela. However, the Cantaure lot of eight adults and six juve-

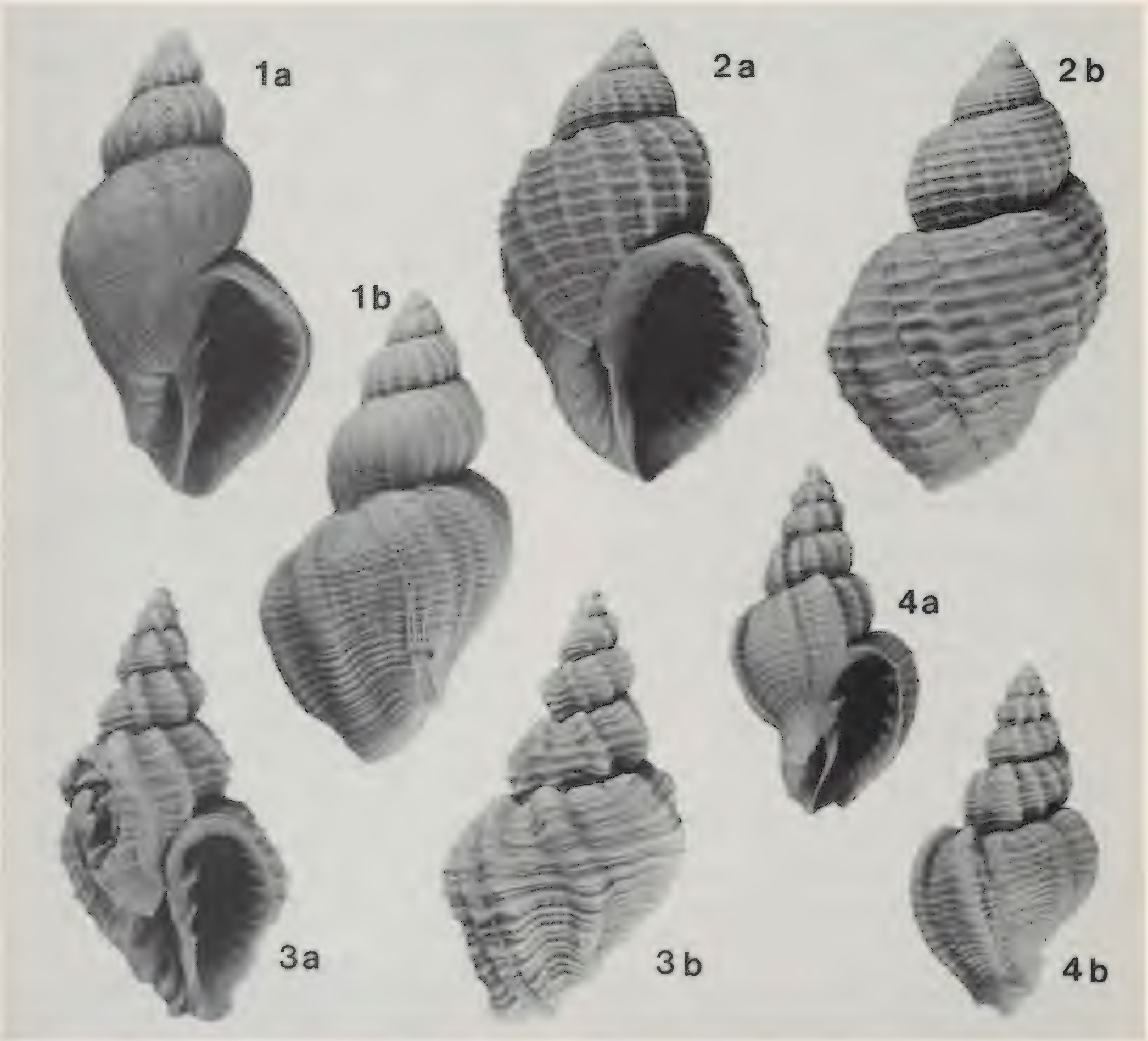

PLATE 1

Figures

1. *Cancellaria (Charcolleria) emilyvokesae* Landau and Petit, n. sp.
   (x 2) NMB H 17787 (holotype): height 26 mm, diameter 18.4 mm.
2. *Cancellaria (Massyla) cantaurana* Landau and Petit, n. sp.
   (x 2) NMB H 17788 (holotype): height 21 mm, diameter 15.5 mm.
3. *Axelella yaro* Landau and Petit, n. sp.
   (x 2) NMB H 17785 (holotype): height 25 mm, diameter 13 mm.
4. *Narona barystoma* Woodring, 1970
   (x 2) NMB H 17786; height 19.5 mm, diameter 10 mm.

Locality of all: NMB 17516, Paraguaná Peninsula, Falcón, Venezuela; Cantaure Formation.

niles represent a fairly variable species. The mean height of adults is 20 mm and width 9 mm (maximum height 21 mm, width 10 mm) suggesting that Woodring's specimens were all juveniles with the exception of the holotype, which is probably sub-adult. The sculpture of the Cantaure specimens tends to become obsolete on the body whorl in most of the adult specimens. One of the adults retains the sculpture of strong axial ribs and spiral threads throughout as does Woodring's holotype, which is elongated with a narrower aperture. Apart from these variable characters, the protoconch, the angled shoulder on the early whorls, the details of sculpture and the structure of the columella are identical.

ACKNOWLEDGEMENTS

The authors would like to express special thanks to Emily H. Vokes for her assistance with the photographic work, editorial assistance, inspiration and unfailing encouragement.

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February 26, 1996

NOTES ON THE MOLLUSCAN FAUNA OF THE MONTEZUMA FORMATION, COSTA RICA

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Only recently has a paper on the Montezuma Formation (Pliocene-Pleistocene of Costa Rica) published in 1986 come to my attention. This paper is by Teresita Aguilar and Rudolf Fischer, with the Gastropoda being by Aguilar and the Bivalvia by Fischer. As faunal studies of this type are used in various compilations for both spatial and temporal ranges of taxa, the present paper is written to point out incorrect identifications of both genus-group and species-group taxa, particularly in the Cancellariidae as well as some others. The cited identifications incorrectly indicate, for example, that Recent deep-water species from the Galapagos Islands once lived in much shallower water during the Pliocene-Pleistocene. The stratigraphic portion of the paper showing ranges of the species studied should send up a warning flag to the reader, as the taxa listed are an eclectic lot, containing species previously known only as endemics from the Alum Bluff Formation of Florida (Miocene), the Tubará Formation of Colombia (Pliocene), deep-water Recent species from the Galapagos Islands, and other unlikely cohabitants.

My particular interest is in the family Cancellariidae and the relevant species in this study are:

Cancellaria (Cancellaria) decussata Sowerby, 1832. The figured specimen (p. 226, pl. 2, fig. 26) does appear to be a species of *Cancellaria* s.s., although the columellar folds are hidden by matrix so this cannot be determined with certainty. However, it is not *C. (C.) decussata*, which is a Recent species ranging from the Gulf of California to the Galapagos Islands and also known from beds in the Galapagos thought to be Pleistocene in age. *Cancellaria decussata* has much finer sculpture, which appears as beading, unlike the specimen figured which is widely reticulate. Also, the Recent shell is not so constricted behind the siphonal fasciole. This Montezuma specimen cannot be positively identified with any described species but it is very close to, if not the same as, *C. corrosa* Reeve, 1856, a rare species living off western Mexico.

Cancellaria (Cancellaria) darwini Petit, 1970. The specimen illustrated (p. 226, pl. 2, fig. 23) is a juvenile *Cancellaria* s.s., probably *C. albida* Hinds, 1843, of the Recent Panamic-Pacific fauna, but positive identification is not possible from the illustration. It is definitely not *C. darwini* which, although placed in *Cancellaria* s.s. by Keen (1971, p. 647), was stated in its original description to lack the strong columellar folds of *Cancellaria* s.s. and should be placed in some subgenus other than the nominotypical. The Recent species is somewhat littoriniform in outline and the shell is weakly cancellate, not beaded as is the Montezuma specimen.

Cancellaria (Agatrix) deroyae Petit, 1970. The figured specimen (pl. 2, fig. 12) is *C.(C.) urceolata* Hinds, 1843, a Recent species which ranges from the Gulf of California to Ecuador. *Cancellaria deroyae,* now properly placed in the genus *Admetula,* is known only from 170-200 meters off the Galapagos Islands and bears no resemblance to the shell figured.

Cancellaria (Euclia) codazzii Anderson, 1929. This species was described from the Tubará Formation (Pliocene) of Colombia and has been reported from various deposits in Central America. The figured Montezuma specimen (pl. 3, fig. 24) is not *C. codazzii*, which has a tabulate shell without strong nodes at the shoulder and is more constricted anteriorly than the specimen figured. The Montezuma specimen has the general shape and sculpture of *C. cassidiformis* Sowerby, 1832, a shallow-water Recent species ranging from the Gulf of California to Peru and is probably that species.

A fifth member of the Cancellarioidea figured in this paper (pl. 2, fig. 22) is *Tritonoharpa siphonata* (Reeve, 1844), which appears to be correctly identified, although cited as a *Colubraria*, which was the usual placement when the paper was written.

A detailed critique of the identifications of the Montezuma specimens figured in this paper is not being attempted. However, workers are cautioned about citing taxa from this work without examining the taxa closely. Besides the cancellariids

listed above, some obvious errors in identification of other gastropods are:

In the stratigraphic portion of the paper (p. 214) it is pointed out that the genus *Marginella*, although occurring in the Montezuma fauna is not present in the Recent Panamic-Pacific fauna. This statement is based upon a species listed and figured (p. 226, pl. 2, fig. 19) as *Marginella mindiensis* Cossmann, 1913. The figured specimen is not a *Marginella* but is a *Prunum*. The only reference cited is that of Olsson (1922, p. 268), who placed the species in *Marginella*, as had Cossmann originally. No mention is made of Woodring's treatment of this species (1970, p. 332, pl. 51, figs. 10, 11), although his work is cited as a reference. Woodring placed this taxon in the synonymy of *Prunum gatunense* (Brown and Pilsbry, 1911) and referred to a similar unnamed species living off Costa Rica. The Montezuma specimen may be *Prunum gatunense*, but in any case the genus *Marginella* does not occur in the Montezuma Formation as stated.

Plate 2, fig. 8, is labeled as *Distorsio (Rhysena) floridana* (Gardner). The figured specimen is not the Alum Bluff (Miocene) species described by Gardner.

Plate 2, fig. 11, is labeled *Cymatium* cf. *wiegmanni* (Anton) but it is a *Distorsio*, not a *Cymatium*.

Plate 2, figs. 15 and 16, are labeled *Eupleura* sp., but the figures are of a cymatiid.

Plate 2, fig. 17, is said to be *Eupleura lehneri* Jung, which was described from the late Miocene of Trinidad, but the specimen is the Recent eastern Pacific *E. muriciformis* (Broderip, 1833).

Plate 2, fig. 18, is identified as the Gatun Formation species *Typhis (Pilsbrytyphis) gabbi* (Brown and Pilsbry) but is the Recent eastern Pacific *Haustellotyphis cumingi* (Broderip, 1833).

In addition to the two cancellariids identified as endemic deep-water Galapagos species, a third species is also so treated. It is said to be *Compsodrillia gracilis* McLean and Poorman and is represented (pl. 3, fig. 26) by a badly broken shell lacking its apex, at least one third of its body whorl, and the anterior portion. Because of the presence in the Recent Panamic-Pacific fauna of similar species, the precise identification of this partial specimen should be examined by turrid specialists before admitting this taxon to a shallow to moderate depth Pliocene-Pleistocene fauna in Costa Rica.

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NOTES ON THE FAUNA OF THE CHIPOLA FORMATION – XL
A NEW SPECIES OF THE GENUS *CERITHIUM* (MOLLUSCA: GASTROPODA)

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Since Shirley Hoerle published her paper on the Cerithiidae and Potamididae from the Chipola Formation in *Tulane Studies in Geology and Paleontology* (1972, v. 10, no. 1, pp. 1-22) a new species of *Cerithium* has been discovered by two different fossil collectors. The distribution of this new species is limited to the lower Chipola Formation deposits at Alum Bluff and the lower deposits along the Chipola River. It is relatively common at Alum Bluff but rare along the Chipola River and at both localities it is extremely difficult to collect because drought conditions must exist in order to gain access to the deposits where it is found. Over the intervening years, however, a sufficient number of shell fragments have been collected to allow the investigator to describe this *Cerithium* as a new species.

Family CERITHIIDAE Fleming, 1822
Subfamily CERITHIINAE Fleming, 1822
Genus CERITHIUM Bruguière, 1789

Cerithium Bruguière, 1789, Encycl. Meth. (Vers), v. 1, p. XV (genus without species); 1792, *ibid*, p. 467.

Type species: *Cerithium adamsonii* Bruguière (= *Cerithium erythraeonense* Lamarck, 1822), by virtual tautonymy.

CERITHIUM LOUISAE
Schmelz, n. sp.
Plate 1, figures 1-3

Diagnosis: Shell solid, nuclear whorls absent. Approximately eleven noded teleconch whorls. Five spiral rows of strongly noded costa on body whorl, the first row of nodes transformed into thirteen stout spines, each arching upwards beyond the shoulder. Raised axial ridges crossing sutural ramp and connecting spines to a well-developed, appressed suture. Varix only on body whorl. Each remaining teleconch whorl with a peripheral row of spines and two spiral rows of strongly noded costa. Pillar short, arched. Canal narrow, deep, recurved. Inner lip of aperture with strong callus, edge free; outer lip thickened, arched, with crenulations along edge corresponding to spiral sculpture; at junction with body a moderate sinus and subsutural, elevated ridge developed, entering throat of shell.

Holotype: UF 71293; height 42.1 mm, maximum diameter 21.1 mm.

Type locality: TU 1545, Chipola Formation, Cooter Bluff, sharp westward bend on west bank of Chipola River about 1,000 feet below mouth of Taylor Lake Branch (NW 1/4 Sec. 29, T1N, R9W), Calhoun County, Florida.

Paratype A: UF 71294; height 46.1 mm, maximum diameter 23.0 mm. Locality: TU 453, Alum Bluff (lower beds), Apalachicola River (NE 1/4 Sec. 24, T1N, R8W), Liberty County, Florida.

Paratype B: UF 71295; height (incomplete) 18.0 mm, maximum diameter 8.5 mm.Locality: TU 453, Alum Bluff (lower beds), Apalachicola River (NE 1/4 Sec. 24, T1N, R8W), Liberty Co., Florida.

Additional unfigured paratypes: Five from TU 453 (two from the Murray collection and three from the Compton collection).

Etymology: Named for Louise Compton, Marietta, Georgia, a longtime collector of Florida fossils, who generously made specimens from her collection of Chipola material available for study.

Discussion: Although no complete specimen of *Cerithium louisae* has been discovered, it is estimated from shell fragments that this species achieved a height in excess of 70 mm and was probably comparable in size to the large Chipola species *Cerithium burnsii*. The deposits in which the new species is found suggest that it lived in shallow tropical waters near coral reefs.

Cerithium louisae is a very ornate and distinctive species whose closest fossil and living counterpart appears to be *Cerithium nodulosum* from the Indo-Pacific. The latter species has been recorded from the Late Miocene deposits of Bikini Atoll in the Marshall Islands, the Neogene of Palau, and from the Plio-Pleistocene of Guam (Houbrick, 1992, p. 134). According to Houbrick (1992, p. 132), and the personal observations of this investigator, *C. nodulosum* is found shoreward of the reef face on intertidal and subtidal rocky shelves.

ACKNOWLEDGMENTS

This investigator would like to extend a special note of thanks to Emily Vokes for her assistance with the photographic work. Additional notes of appreciation are also extended to Louise Compton and Andrew and Greta Murray for their contribution of specimens.

LOCALITY DATA

The following are Tulane University Chipola Formation fossil localities:

453. Alum Bluff (lower beds), Apalachicola River (NE 1/4 Sec. 24, T1N, R8W), Liberty Co., Florida.

1545. Cooter Bluff, sharp westward bend on west bank of Chipola River about 1,000 feet below mouth of Taylor Lake Branch (NW 1/4 Sec. 29, T1N, R9W), Calhoun Co., Florida.

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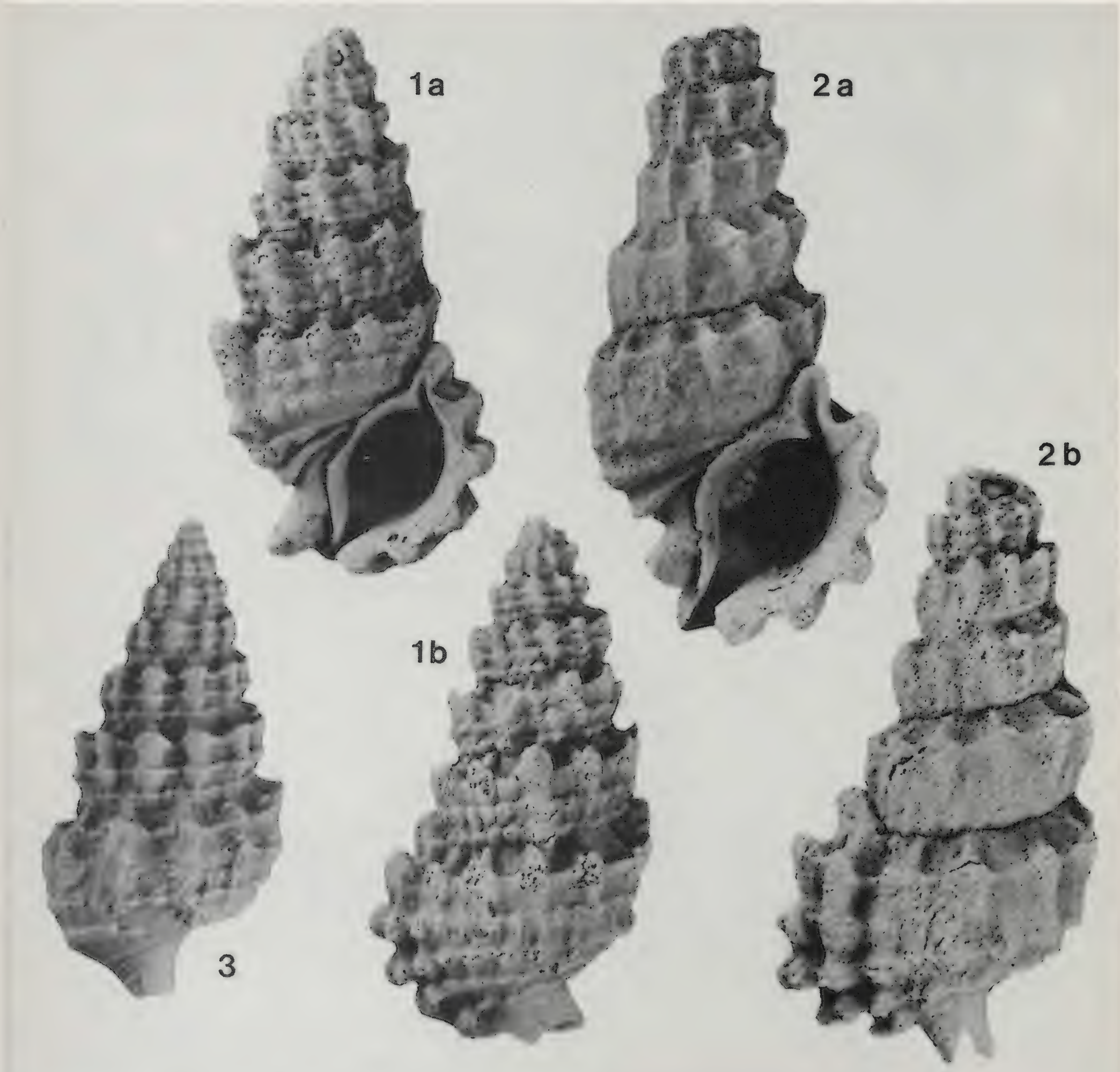
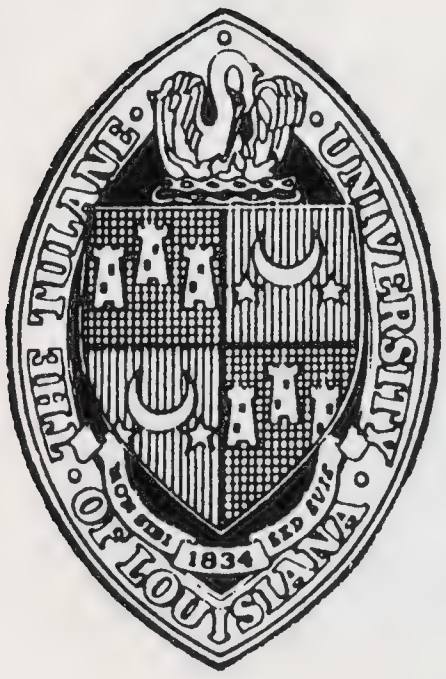


PLATE 1

Figures 1-3. *Cerithium louisae* Schmelz, n. sp.

1. (X 1-1/2) UF 71293 (holotype); height 42.1 mm, diameter 21.1 mm; locality TU 1545, Chipola Formation, Florida.
2. (X 1-1/2) UF 71294 (paratype A); height 46.1 mm, diameter 23.0 mm; locality TU 453, Chipola Formation, Florida.
3. (X 3) UF 71295 (paratype B); height (incomplete) 18.0 mm, diameter 8.5 mm; locality TU 453, Chipola Formation, Florida.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Volume 30

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HUBERT C. SKINNER

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TULANE STUDIES IN GEOLOGY AND PALEONTOLOGY

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THE SALT MOUNTAIN LIMESTONE OF ALABAMA

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ABSTRACT

The Salt Mountain Limestone of southwestern Alabama is a Late Paleocene (Thanetian) tropical-subtropical, photic-zone reef constructed primarily of sponges, coralline red algae, and lime mud, but with common scleractinian corals (12 species) and abundant bryozoa. Accessory fauna includes larger and smaller benthic foraminfera, echinoderms, endolithic bivalves, and brachiopods. The reef developed on an inner neritic siliciclastic shelf, probably over a local diapiric shoal, at an approximate paleolatitude of 31°-32° North. The final demise of the reef was evidently caused by siliciclastic influx from the prograding Holly Springs Delta System of the Mississippi Embayment. This massive carbonate underwent several episodes of diagenetic alteration, including early marine micritic cementation.

Smaller benthic foraminifera assemblages suggest depositional water depths of 15-30 meters for forereef sediments, to less than 5 meters for the reef core. The dominant alga is *Archaeolithothamnium*, which occurs as both thick and thin crusts, and rhodoliths, suggesting water depths between 5-20 meters. At least 15 distinct sponge morphotypes are consistently identified, ranging from small, 2 -10 cm oblong buds to large, vase- or barrel-shaped forms that may have reached 1 meter in length. Echinoderms are extremely abundant, as indicated by ossicles and plates, but only six species of regular echinoids have been identified. Conspicuously absent are any remains of irregular echinoids, which may not have occupied reef niches at that time as they clearly did by the Late Eocene and Early Oligocene.

The constructional dominance of coralline algae and sponges in the Salt Mountain could be an indication that scleractinians had not yet fully established their post-Cretaceous role as primary reef framestone builders in the Gulf of Mexico Basin. The abundance of hexactinellid sponges, however, may be especially significant. The siliceous hexactinellids are exclusive K-strategists, requiring stable environments, but are bathymetrically tolerant. They reached their greatest diversity in the Late Cretaceous and were common reef/mound constructors in the Jurassic. Their presence in the Salt Mountain suggests a temporary role as early post-Cretaceous photic-zone reef constructors prior to the full recovery of scleractinian-dominated reefs in the later Paleogene.

PART I
INTRODUCTION TO THE SALT MOUNTAIN LIMESTONE

JONATHAN R. BRYAN

I. OVERVIEW

In the 57 years since the publication of Lyman Toulmin's monograph, "The Salt Mountain Limestone of Alabama" (*Geological Survey of Alabama Bulletin 46*), there has been surprisingly little research on this fossiliferous Gulf Coast formation. Perhaps this is because the formation is locally restricted in outcrop and, therefore, considered to be of minimal stratigraphic importance (it is entirely omitted in many regional stratigraphic surveys–*e.g.* Gibson *et al.*, 1982; Mancini, 1984; Mancini and Tew, 1991). Or possibly because this carbonate buildup appears to be recrystallized and largely non-fossiliferous.

But thin-section analysis and careful collecting along the outcrop have uncovered a diverse, undescribed biota of coralline red algae, siliceous sponges, and corals. The collection of papers in this volume deals with various aspects of the Salt Mountain Limestone, and is intended as a resource for continuing research. It reviews past research and summarizes current investigations on the stratigraphy, paleontology, and paleoecology of the Salt Mountain. These papers are not exhaustive. In particular, systematic treatment of the diverse sponge fauna is still in progress. Coralline algae and bryozoa are also largely unstudied. But the broader paleobiological significance of the Salt Mountain biota is clear. The age and reefal character of the Salt Mountain give it a unique significance with regard to the post-Cretaceous evolution of reef communities.

The publication of these articles coincides with a fieldtrip scheduled for March 26, 1997, in conjunction with the 46th annual meeting of the Southeastern Section of the Geological Society of America at Auburn, Alabama, and is sponsored by the Southeastern Section of the Paleontological Society. Special thanks go to Emily Vokes for her cooperation and guidance in the preparation of this special collection of articles.

II. GENERAL DESCRIPTION

The Salt Mountain Limestone is a muddy, soft to well-indurated, reefal carbonate of Late Paleocene age, located in southwestern Alabama. It is composed of several lithologies, including bioclastic packstones/floatstones, algal and sponge-algal boundstones, sponge bafflestones, and coral framestones. Toulmin (1940b, p.30) described the Salt Mountain in outcrop as "hard white crystalline limestone forming irregular ledges 2 to 8 feet thick, and beds or lenses of soft white limestone." The extreme hardness of most of the rock gives it a cherty appearance and texture. But silica makes up only a small fraction of the composition of both soft and hard lithologies (Toulmin, 1940b). The "cherty" texture results from the abundance of micritic cements.

The Salt Mountain is densely fossiliferous, although this is not immediately evident on the outcrop. There is a rich microfauna in the less indurated beds, including foraminifera, ostracods, bryozoa, and brachiopods. Framebuilding coralline algae, sponges, and corals are most evident in thin-section, but are also common in outcrop. *In situ* corals may reach over 1 meter in diameter. Sponges range in size from 1-2 cm to large fragments of barrel-shaped sponges that may have approached 1 meter in length. Most solitary sponges range from 2-10 cm in size. Extensive, anasthomosing sponge networks can be seen in several areas along the top of the outcrop. The sponges are generally preserved as micritic casts.

The Salt Mountain has been unanimously recognized as a reefal limestone because of the presence of fairly large colonial corals. Smith and Johnson (1887, p.21) mentioned "great masses of corals" which "make up a very considerable portion of the hill". Langdon (1891) described the Salt Mountain as "an atoll built up in Tertiary seas." And according to Toulmin (1967, p.88), "The limestone hill called Salt Mountain once had a coral reef along the top. The reef has been removed by

zealous collectors." Large coral colonies are now fairly rare, but can still be collected along the top of the outcrop.

The scleractinian corals, however, are not the primary reef constructors. Although not recognized by these early geologists, coralline red algae and sponges are by far the volumetrically dominant contributors to the buildup. The massive nature of the limestone, and its micritic composition, obscure this fact when making outcrop observations. Furthermore, the sponges are primarily the siliceous hexactinellids, a group that today is largely restricted to deep and/or cold waters. Yet the Salt Mountain clearly developed in photic-zone, tropical-subtropical Late Paleocene waters–a time when scleractinian-dominated reefs had still not yet recovered from the effects of the terminal Cretaceous extinction event. The unique organic construction of the Salt Mountain reef makes it especially deserving of paleoecologic research, particularly with respect to its importance for our understanding of the evolution of post-Cretaceous reef communities.

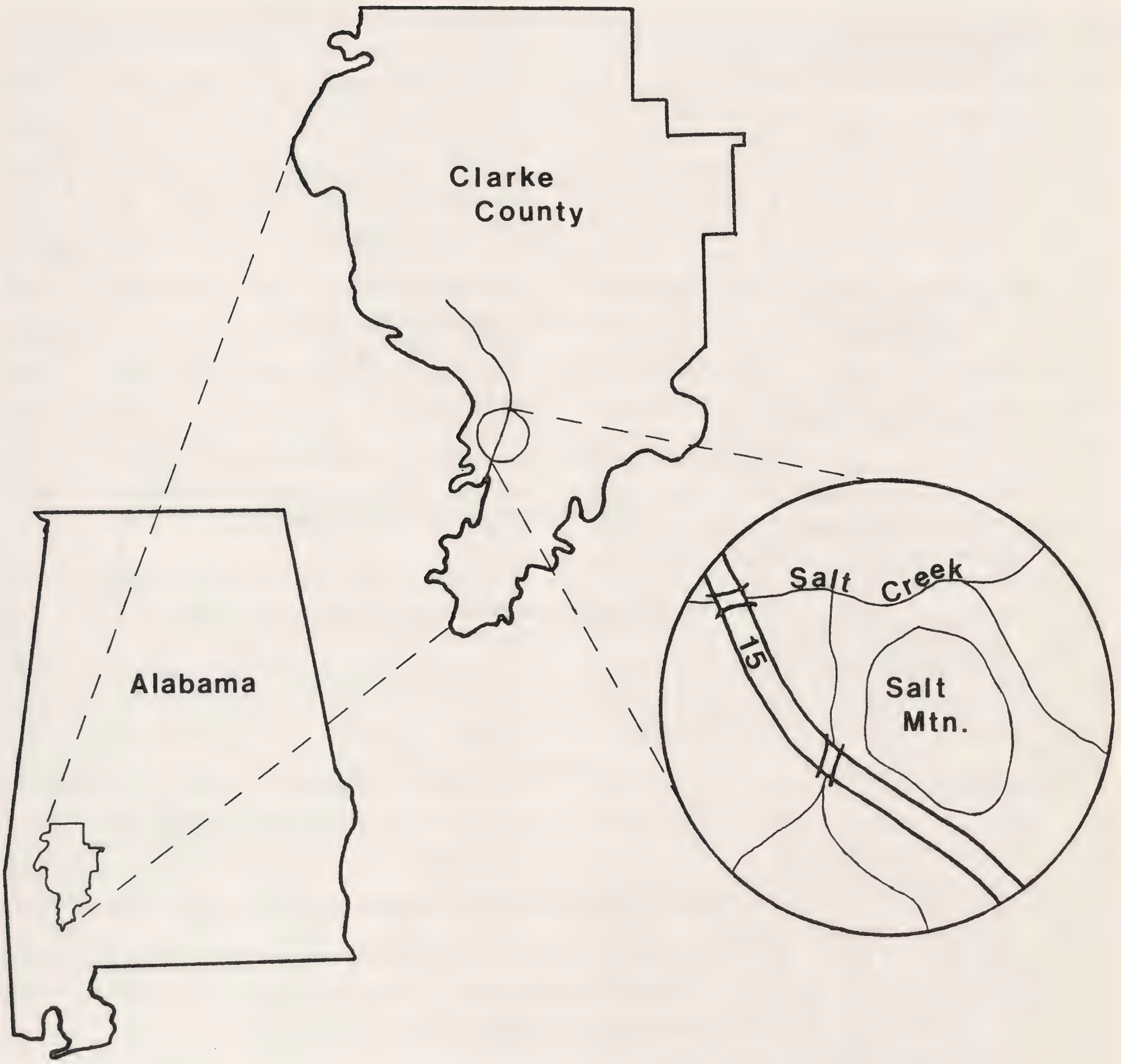
III. TYPE AREA AND REGIONAL OCCURRENCE

The type locality and only significant exposure of the Salt Mountain Limestone is located about 9.6 km (6 miles) south of Jackson, Clarke Co., Alabama, on County Highway 15 (sec. 33, T6N, R2E; Text-figure 1)(see Causey and Newton, 1972). The approximately 40 meters (130 feet) of limestone exposed here was brought to the surface on the upthrown block of the Jackson Fault (with a minimum displacement of over 400 meters [1,312 feet]; Toulmin, 1940b). The strata dip to the east from 8 to 10 degrees. This uplift was associated with the growth of the Klepac Salt Dome (Louann Salt, Jurassic in age), which is one of the easternmost surficial expressions of salt dome intrusion in the Gulf of Mexico Basin. Organic construction of the reef was probably facilitated by local shoaling resulting from dome development. Both Upper Cretaceous and Tertiary sediments thin across the Klepac Dome (Joiner and Moore, 1966; Moore, 1971).

The Salt Mountain Limestone has been reported from the subsurface of southeastern Mississippi, southwestern Alabama and the Florida panhandle (Toulmin, 1955; Murray, 1961; Rainwater, 1964; Maher and Applin, 1968; Bryan, 1991, fig.3). Reported thicknesses are variable and the formation may be discontinuous. There appears to be an increase in thickness in northern Florida near what was the flanks of the Suwannee Channel, a current-swept strait that flowed across north Florida and south Georgia from the Cretaceous through the Oligocene (Popenoe *et al.*, 1987). The Salt Mountain is 21 to 27 meters (70 to 90 feet) thick in Walton and Bay Counties, Florida, but is absent near the coast in Gulf County and in the Tallahassee area (*i.e.*, the axis of the Suwannee Channel) (Toulmin, 1955).

The flanks of Suwannee Channel were frequently the location of organic and reefal buildups (Chen, 1965; Manker and Carter, 1987; Pinet and Popenoe, 1985), although it is unknown if the Salt Mountain here or in other subsurface areas represents the reef facies. The subsurface Salt Mountain is usually recognized by its foraminiferal fauna, and published lithologic descriptions are of limited use. It seems probable that the subsurface Salt Mountain may at best resemble Biofacies 1 as seen at the type section. Cole (1944, pl.12) illustrates a thin section from samples of the Salt Mountain taken from a core in Jackson County, Florida. The lithology appears to be a grainstone, and is rich in *Discocyclina* and bryozoa, but seems to lack algae.

According to Toulmin (1955) the Salt Mountain becomes conformable with the Early Paleocene (Danian) Clayton Formation in the subsurface of southeastern Alabama. This is significant from the standpoint of facies development in that the upper Clayton in this region (as seen along the Chattahoochee River near Fort Gaines, Georgia, and at Rutledge, Alabama) is a rhodolith limestone very reminiscent of the Salt Mountain, and contains a smaller foraminiferal and brachiopod fauna with strong affinities to that of the type Salt Mountain (Toulmin, 1941; Bryan, 1993). This time-transgressive aspect of the Salt Mountain and upper Clayton formations was evidently the source of much early confusion and miscorrelation (MacNeil, 1946).



Text-figure 1. Type locality of the Salt Mountain Limestone, located approximately 10 km south of Jackson, Clarke County, Alabama (sec. 33, T6N, R2E). Trace of Jackson Fault is illustrated on Clarke County outline (from Bryan, 1991).

IV. EARLY INVESTIGATIONS AND BIOSTRATIGRAPHY

The Salt Mountain was first described by Smith and Johnson (1887) as the "Coral Limestone," the uppermost division of their single formation, the "White Limestone," which included the lower "Jackson" and middle "Vicksburg (orbitoidal)" divisions. Smith and Johnson (p.20) described 46 meters (150 feet) of "Coral Limestone" at Salt Mountain–"The rock here, is a hard, white limestone, composed in great measure of masses of coral partly silicified. Near the base of this rock there occur great numbers of the spines and plates of echinoderms." The formation was first referred to as the "Salt Mountain limestone" by Langdon (1891).

Working before the discovery of the Jackson Fault, and prior to the full recognition and correlation of the Paleocene and Oligocene systems, these early workers thought that the Salt Mountain overlay what are now known to be Oligocene (Vicksburgian) carbonates, and was Eocene in age. Indeed, faulting has juxtaposed the Salt Mountain into a position of

apparent superposition over Vicksburgian carbonates (see Toulmin and Newton, 1963). The displacement and true age of the Salt Mountain was realized after the discovery of the Jackson Fault (Hopkins, 1918), the subsurface stratigraphic position of the Salt Mountain (Blanpied *in* Crider *et al.*, 1932), and the discovery of discocyclinid larger foraminifera (Vaughan, 1936; Cooke, 1935; Toulmin, 1940b). These studies placed the Salt Mountain in the Wilcox Group, then considered entirely Eocene in age. The presence in the Salt Mountain of the index oyster, "*Ostrea thirsae*" [= *Odontogryphea thirsae* (Gabb)] suggested equivalence to the Nanafalia Formation. The Salt Mountain was understood to be the offshore, limey equivalent of the nearshore, sandy Nanafalia Formation (Blanpied, 1938; Toulmin, 1940b, 1967; MacNeil, 1946; Rainwater, 1964). The Salt Mountain is located approximately 80 km (50 miles) south of the nearest outcropping "*Ostrea thirsae* beds" (Toulmin, 1940b).

Loeblich and Tappan (1957) established the Late Paleocene age of the Salt Mountain using planktic foraminifera (assignable to the *Planorotalites pseudomenardii* Zone, = Zone P4; Berggren, 1963, Berggren and Aubert, 1975, Fluegeman, this volume). They considered the Salt Mountain to be older than the Nanafalia Formation and suggested it be placed in the underlying Midway Group. Subsequent work by Wind (1974) and Siesser (1983) on calcareous nannoplankton confirms the Late Paleocene age. Wind and Siesser have both assigned the Salt Mountain to nannoplankton zone NP7 (Text-figure 2), although slightly older than the Nanafalia Formation (Wind, 1974).

Toulmin published his Alabama Geological Survey monograph on the Salt Mountain in 1940 (Toulmin, 1940b) in which he summarized early research, provided a thorough field description of the formation, and gave extensive microfaunal taxonomic lists. Toulmin later commented on the Salt Mountain in field excursion guidebooks (Toulmin, 1962, 1967) and state publications (Toulmin and Newton, 1963; also Causey and Newton, 1972). Toulmin evidently never accepted a Late Paleocene age for the Salt Mountain, but retained it in the Early Eocene (Toulmin, 1962, p.3; 1977, pp.28,90). The earlier placement of the entire Wilcox Group within the Eocene has resulted in many correlations of the Salt Mountain with the Oldsmar Limestone of subsurface Florida (*e.g.*, Toulmin, 1955; Levin, 1957; Chen, 1965).

Bryan (1991), using thin section observations, described 4 biofacies within the Salt Mountain Limestone, and discussed the importance of the Salt Mountain with respect to other Early Tertiary reefs. Finally, Denison *et al.* (1993) included Salt Mountain samples in their study of Paleogene strontium isotope (87Sr/86Sr) variation in seawater, using Gulf Coast material. The Salt Mountain samples proved to be well below expected Paleocene values, but consistent with Cretaceous and older values. Contamination from migrating Mesozoic brines is undoubtedly the cause for the low ratios.

V. GENERAL PALEONTOLOGY

The Salt Mountain Limestone contains a rich, but only partially documented biota. Salt Mountain taxa that have been investigated include calcareous nannoplankton (Wind, 1974; Siesser, 1983), planktonic foraminifera (Toulmin, 1940b; Loeblich and Tappan, 1957), smaller benthic foraminfera (Toulmin, 1940b, 1941; Berggren, 1974; Berggren and Aubert,

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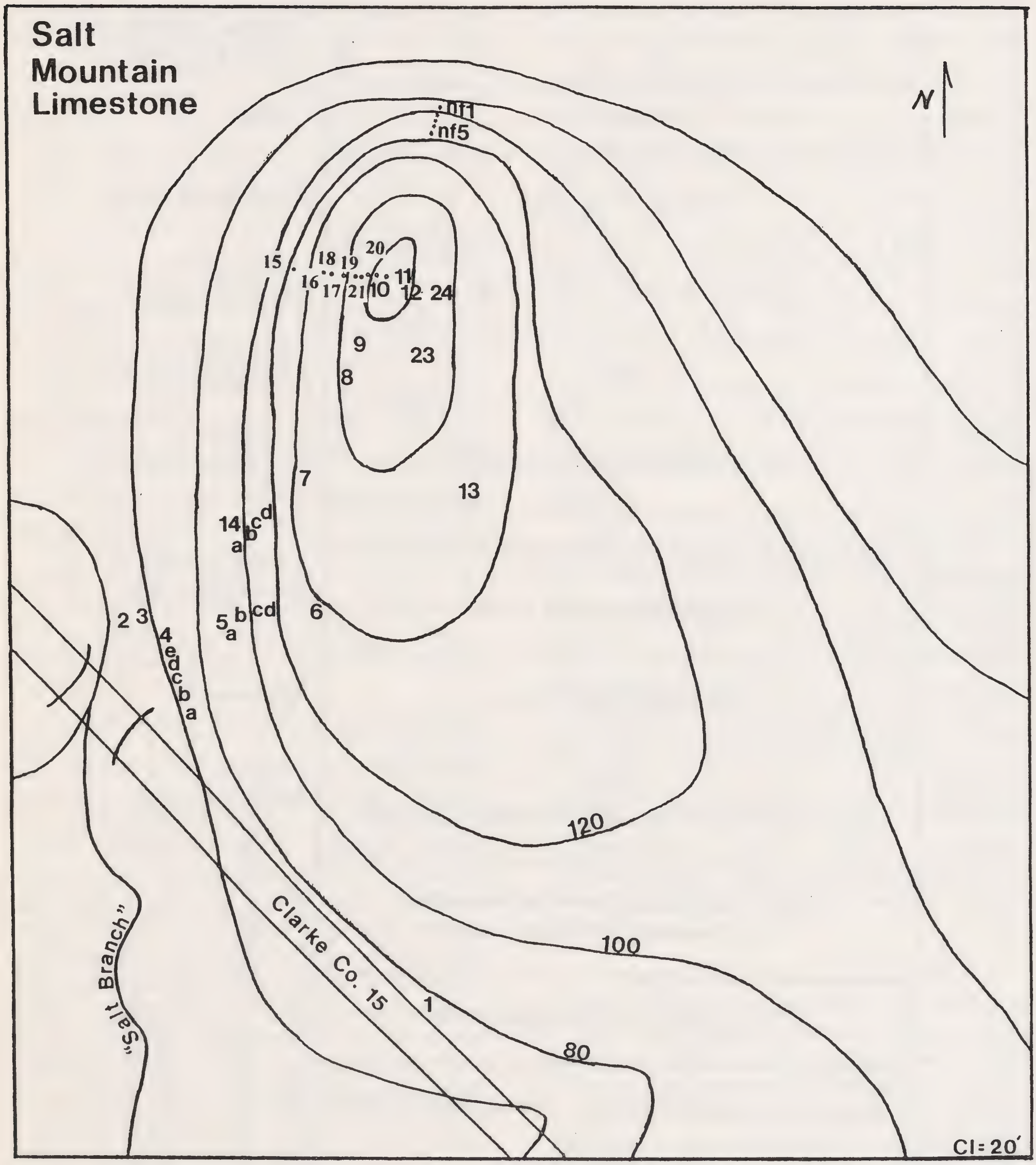
Text-figure 2. Generalized stratigraphy of the Salt Mountain Limestone and regional lithocorrelates. Sources: 1, Haq *et al.*, 1988; 2, Harland *et al.*, 1989; 3, Murray, 1961; 4, Wind, 1974, Siesser, 1983; 5, Loeblich and Tappan, 1957, Berggren, 1963, Berggren and Aubert, 1975; 6, Gravell and Hanna, 1938, Cole, 1959, 1969; 7, Toulmin, 1977; 8, Haq *et al.*, 1988, and this paper; 9, Lindberg, 1988, and others; 10, Toulmin, 1940b, 1977; 11, Chen, 1965, Cole, 1938, Lindberg, 1988; Winston, 1978, 1994.

<58.5	>55	Approx. Radiometric-Derived Age (Ma)(1)
Paleocene		**Epoch**
Selandian/Thanetian		**European Stage (2)**
Wilcox Group/Sabinian Stage		**Gulf Coastal Group/Stage (3)**
NP7		**Calcareous Nannoplankton (4)**
***Planorotalites pseudomenardii* (P4)**		**Planktonic Foraminifera (5)**
Discocyclina weaveri*--*Pseudophragmina stephensoni ***Ranikothalia catenula* Fauna**		**Larger Benthic Foraminifera (6)**
Odontogryphaea thirsae		**Molluscs (7)**
TA 2.1 **Lowstand Carbonate Transgressive Carbonate**		**Sequence Stratigraphy (8)**
Wilcox Formation/Nanafalia Formation (Salt Mountain Limestone locally)		**W/E Mississippi(9)**
SALT MOUNTAIN LIMESTONE		**SW S.Cent–E. Panhandle Peninsula Southern Alabama(10) Florida(11)**
Gravel Creek Sand Member "Ostrea thirsae beds" **Nanafalia Formation**		**Salt Mountain Limestone and Regional Lithocorrelates**
Wilcox Group Undifferentiated (Salt Mountain Limestone locally)		
Cedar Keys Formation		
Rebecca Shoal Dolomite		



Text-figure 3. Sampling locations at Salt Mountain plotted on the topographic map of Toulmin (1940b).

1975; Brisken and Fluegeman, 1990; Fluegeman this volume), larger benthic foraminifera (Vaughan, 1936; Cole, 1959,1969; Bryan this volume), coralline algae (Bryan, 1991; not described), sponges (Bryan, 1991; not described), scleractinian corals (Vaughan, 1900; Stemann this volume), ostracods (Toulmin, 1940b), bryozoa (Toulmin, 1940b; not described), brachiopods (Toulmin, 1940a,b; Stenzel, 1942), echinoids (Cooke, 1959; Carter this volume), and miscellaneous fauna (*viz*, annelids, molluscs, crinoids, vertebrates; Toulmin, 1940b; Bryan, 1991).

VI. DIAGENESIS

The unique organic composition of the Salt Mountain Limestone make its syn- and post-depositional history an especially promising subject for research. The following are only preliminary observations. As already noted, the "cherty" texture of the rock derives from the abundance of micritic cements. In fact, all indurated lithologies have a predominant microspar matrix (probably a neomorphic alteration of original micrite cement). Micrite is sometimes found as thin laminae and frequently fills large cavities, such as spongocoel and the areas surrounding branching corals. The microspar matrix sometimes has a vuggy porosity, with sparse and incompletely developed calcite spar within the vugs. Although the matrix contains most of this secondary porosity, some biochems are also eroded by vugs and many are especially affected along their margins (*e.g.*, coralline algal plates). Subhedral to euhedral Fe-oxides stains are common. Original aragonitic molluscs (especially endolithic bivalves) are preserved as sparry molds with micrite envelopes or as micritic internal molds.

Sponges are preserved as micritic replacements (casts). Spicules within the sponges are completely dissolved, but are nonetheless remarkably preserved as sparry calcite casts (within the micritic body fossil casts). Large coral colonies are also preserved as micritic casts, but details of the septal patterns are often lost (with spar filling corallite voids). Some corals do retain their septa as spar replacements, surrounded by micritic molds (mud infill of interseptal spaces). In outcrop, massive colonies of *Stylophora ponderosa* may quickly grade into otherwise nondescript mudstone, showing how secondary alteration has largely destroyed much of the original reef fabric.

Several syn-depositional and post-depositional diagenetic events are recognizable. There is abundant evidence for early marine, micritic cementation. Most thin sections show regular fracturing of microspar matrix. These fractures are filled with additional micrite/microspar, micritic intraclasts, or a combination of these with calcite spar. Fine laminated micrite may be observed in abrupt, truncated contact with coarse debris (forming small "angular unconformities"), then covered by additional mud, with an iron-oxide contact between the two layers. Also, large, bored lithoclasts sometimes compose the core of algal boundstones and rhodoliths, indicating earlier phases of syn-depositional cementation. Geopetal structures are common and meteoric influence (perhaps more than one phase) is also evident.

VII. REGIONAL PALEOENVIRONMENTAL SETTING

The Late Paleocene was a period of increased warming in an ice-free global ocean. This warming culminated in the Early Eocene, probably the warmest interval in the Cenozoic (Kennett, 1982; Crowley and North, 1991). There were rapid and short-lived temperature increases of 10°C or more in global deep water and high latitude surface waters, resulting in severe extinctions in deep water microfaunas (the "Late Paleocene Thermal Maximum", Zachos *et al.*, 1993; Kennett and Stott, 1991). But low latitude surface waters were evidently unaffected by these temperature excursions, and may not have been significantly different than the present (Adams *et al.*, 1990; Bralower *et al.*, 1995).

In the Gulf Coastal Plain of the southeastern United States, tropical to subtropical conditions are indicated. According to Wolfe (1978), Late Paleocene (lower Wilcox Group) leaf assemblages of the Mississippi Embayment (35°N) represent megathermal (paratropical) Tropical Rain Forest conditions in terrestrial environments of the northern Gulf Coast. In the marine environment, Palmer (1967) considered most Paleocene and Eocene molluscan assemblages of the Gulf Coast to be tropical or subtropical forms. The Salt Mountain reef clearly indicates tropical to subtropical marine conditions, although probably representing the northern extent of such environments.

The Salt Mountain reef developed on an otherwise siliciclastic shelf setting. According to the paleogeographic maps of Stephenson (1928, fig.4), Chen (1965, fig. 42), Rainwater (1964, fig. 9), Gallaway *et al.* (1991, fig. 15), Mancini and Tew (1993, fig. 1), Huddlestun (1993, fig. 50), and Smith *et al.* (1994), the Salt Mountain must have developed within an inner ner-

itic shelf setting, not far from the influence of the Wilcox deltaic sedimentation, and at an approximate paleolatitude of 31°-32° North. During the Late Paleocene, the extensive Holly Springs Delta System covered some 160,930 square km (100,000 square miles) of Louisiana and Mississippi and prograded basinward in three phases with four lobal complexes, developing growth faults, mobilizing salt, and depositing up to 1500 meters of siliciclastics (Gallaway, 1968; Gallaway *et al.*, 1991). The Salt Mountain developed contemporaneously, just to the east of the Holly Springs delta complex, at the eastern extreme of the Mississippi Salt Basin (Martin, 1978, figs. 4,5; Ewing, 1991, fig. 8, pl. 2).

It is likely that the Salt Mountain reef developed on a local shoal, resulting from Klepac Salt Dome development. The Salt Mountain rests on the siliciclastic Naheola Formation. The base of the Salt Mountain is a thin (3-10 cm), glauconitic, calcareous, fossiliferous sand. This sand sharply overlies massive, gray carbonaceous clays and sands of the Naheola Formation (Toulmin, 1962). So the Salt Mountain reef did not develop over an antecedent carbonate (as do many reefs), but appears to have been a carbonate cap–a small bank–which grew over a siliciclastic shoal. Reefal buildups of Cretaceous and Tertiary age are reported from several topographic highs in the Gulf Coast, such as the Sabine Arch of Louisiana and Mississippi, the Jackson Dome of central Mississippi, the Wiggins Uplift of southern Mississippi and Alabama, and numerous salt domes in Louisiana and Texas (Murray, 1961, figs. 6.33, 6.34, 6.36, 6.43, p.107, 361, 386, 392; Frost and Schafersman, 1978; Forman and Schlanger, 1957; Coleman, 1983).

Bryan (1991) compared the Salt Mountain reef to the modern Flower Garden Banks of the northwestern Gulf of Mexico. Both the Salt Mountain and the Flower Garden reefs developed over salt diapirs on siliciclastic-dominated shelves. On the modern Texas-Louisiana shelf, these prominences rise above turbid bottom waters of seasonally variable salinity and temperature (influenced by runoff from the Mississippi River and winter mixing), into clear subtropical to tropical waters originating from the Caribbean with winter temperature minima of only 19° to 20° C (the water column remains stratified and little influenced by winter mixing). Such conditions are suitable for coral-algal reef growth, although because these reefs are near the northern limit for tropical reefs (at 27°N), hermatypic coral diversity is much lower than typical Western Atlantic reefs (Rezak *et al.*, 1985, 1990).

To the south and southeast of the Salt Mountain type area, glauconitic and calcareous shales and sands (Wilcox Group, undifferentiated) formed in much of the Florida panhandle (Chen, 1965) while a large carbonate platform (Cedar Keys Formation, largely an evaporitic dolostone) developed over peninsular Florida. Winston (1978, 1994) reports a dolomitized barrier and atoll reef around much of southern peninsular Florida (Rebecca Shoal Dolomite), equivalent, in-part, with the Cedar Keys Formation. The organic structure of formation is not known.

PLATE 1

Coralline algal bindstone/floatstone, from Biofacies 1. Specimens deposited at Okaloosa-Walton Community College.

Figures

1. Large rhodolith, encrusting over sponge (not seen). Size: 15 cm (long dimension). OW 00113.
2. Floatstone composed of thin, broken algal plates. Size: 19 cm (long dimension). OW 00114.
3. Thick-crusted algal boundstone with lithophagid bivalve boring (l). Size: 5.8 cm (long dimension).
4. Thin section of algal boundstone. Size: 5.5 mm (long dimension).

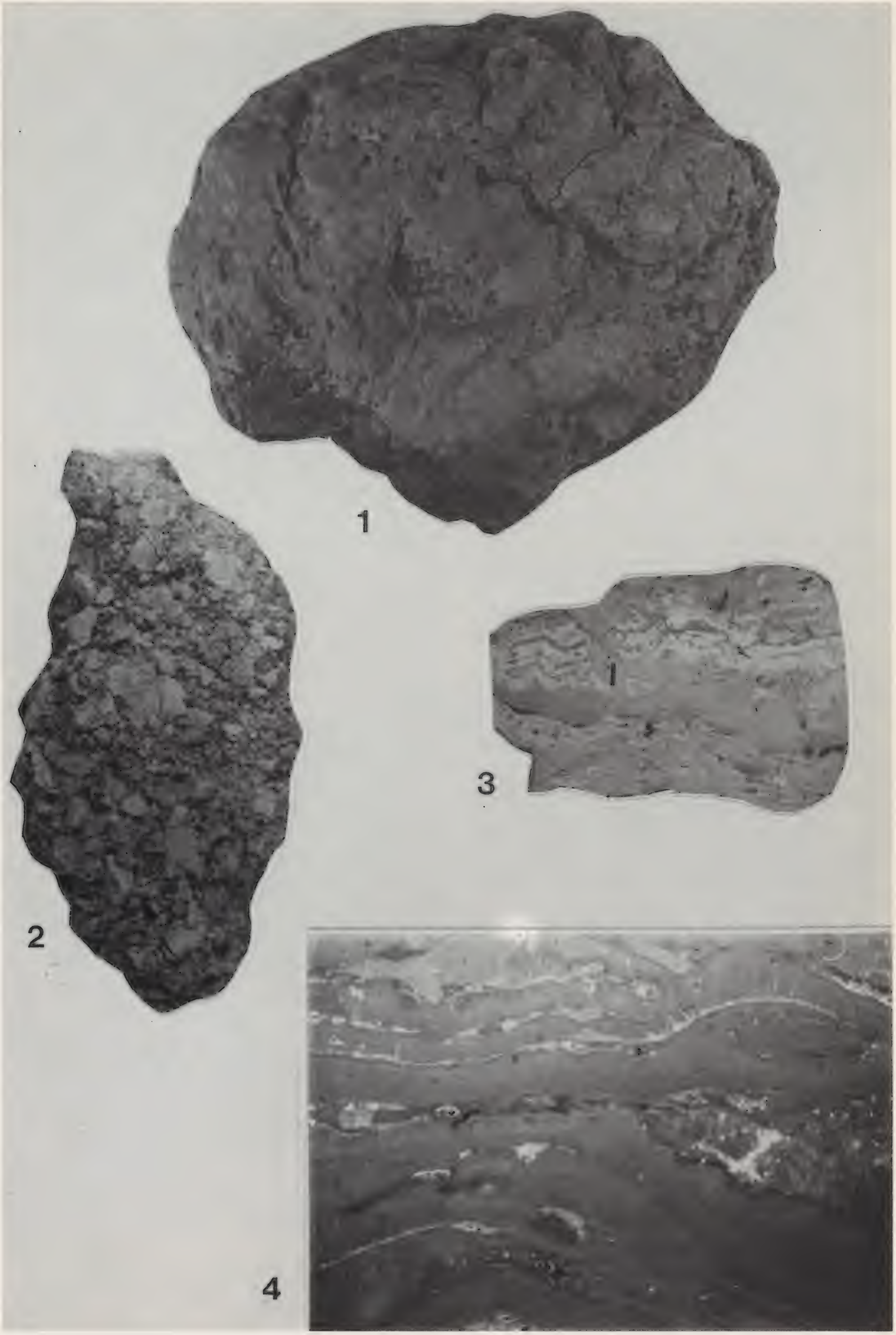


PLATE 1

VIII. SALT MOUNTAIN LIMESTONE BIOFACIES

Bryan (1991) recognized four biofacies on the basis of thin section examination and field relationships. Recent re-sampling of additional outcrops (Text-figure 3) along the mountain has confirmed the consistent presence of these biofacies, but has also shown that lithologic variability is greater that originally reported. Biofacies boundaries are not distinct or consistent, and facies grade laterally as well as vertically. Although some bedding is evident in the outcrop (usually between soft and harder limestone), the formation is essentially massive. The four biofacies of Bryan (1991) are briefly summarized below. The original biofacies names have been modified to reflect the classification of reefal limestones as summarized by James (1983, 1984).

Biofacies 1: Foram-Bryozoan-Algal Bindstone/Floatstone.

Laminar, thin-to-thick encrusting calcareous red algae (mostly *Archaeolithothamnium*) and bryozoans with larger foraminifera (discocyclinids) within micritic matrix. Accessory fossils include planktonic foraminifera, small and large sponges, branching corals, molluscs, echinoderms, and small corals. Biofacies 1 is the volumetrically dominant rock type in the Salt Mountain. Thick-crusted (up to 0.5 cm for individual layers) algal bindstone and rhodoliths are common, but the corallines predominantly occur as very thin, usually fragmented crusts (Plate 1). Thin laminae may extend laterally for several centimeters over micritic substrate.

Biofacies 2: Coral Bafflestone.

Small, delicate, branching corals in micritic matrix. Other allochems include smaller foraminifera, bryozoans, small sponges, and common regular echinoid spines. Coralline algae are rare in this facies, but are found encrusting the branching corals. Larger foraminifera are also uncommon. This biofacies is very similar to Biofacies 4, but appears to have less echinoderm, algal, and (miliolid) foraminifera biochems.

Biofacies 3: Sponge-Coral Bafflestone/Framestone.

Sponges in micritic matrix with massive corals. Coralline red algae are rare to common. Planktonic foraminifera are regularly seen in the micrite. At Stations 13, 21, and 24 (Text-figure 3; and Krumm, this volume), large patches dominated by the coral *Stylophora ponderosa* can be seen *in situ*. The massive coral *Actinacis alabamensis* is less dominant, but still common (Plate 2).

Biofacies 4: Coral-Echinoderm Bafflestone/Floatstone.

Coarse echinoderm debris (spines and ossicles) and branching corals in micrite. Bryozoans and red algae are also common, the algae frequently encrusting echinoderm biochems. Larger foraminifera are rare but miliolid foraminifera are present. Laminated micrite is common and is often seen in abrupt contact with coarse echinoderm debris, suggesting early marine cementation. Biofacies 4 is compositionally similar to Biofacies 2. It is found only at the highest peak of the outcrop.

Additional Biofabrics.

There are additional biofabrics within the Salt Mountain which, although not abundant, are common. There are micritic laminites, for example, possibly of stromatolitic origin, and several samples of white mudstones with "mesoclotted" fabric may be thrombolites. There are also regular occurrences of rhodoliths (Plate 1). These rhodoliths seem to always have large fossils or lithoclasts as cores, with comparatively thin coatings of coralline algae. These round algal boundstones, however, are usually not completely, concentrically encrusted by coralline algae. So there would appear to have been minimal movement on the substrate caused either by

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PLATE 2

Dominant scleractinian corals of the Salt Mountain Limestone, from Biofacies 3. Specimens deposited at Okaloosa-Walton Community College.

Figures

1. Colony of *Stylophora ponderosa*. Size: 18 cm by 12 cm. OW 00115.
2. Colony of *Actinacis alabamensis*. Size: 19 cm by 10 cm. OW 00116.

PLATE 2

currents or bioturbators. But the overall rarity of rhodoliths, the incomplete development of existing rhodoliths, and the thinness of most algal crusts, indicate that the bulk of the Salt Mountain reef developed predominantly below wave base.

At sampling Station 21 a very large, well-preserved, *in situ* colony of *Stylophora ponderosa* was recently discovered (Text-figure 4). This area was more extensively sampled using a meter-grid system (similar to that used by Krumm, this volume) in order to document the organic construction of the reef at a finer scale of analysis. The 5 x 2.5 meter grid with sample locations is shown in Text-figure 5. Table 1 provides lithologic descriptions.

The lithologies within the grid at Station 21 are like those across the rest of the outcrop, and can be easily classified as either Biofacies 1 or 3 as described above. The dominant lithology is an algal and sponge-algal boundstone (mostly Biofacies 3), with abundant bryozoan- and bryozoan-algal rich biomicrite (Biofacies 1). Rare but large coral growth occurs only in one area and coral diversity is lower than in the grid described by D. Krumm (this volume).

IX. CORALLINE ALGAE AND SPONGES

Two groups that are of special interest with regard to reef construction are the coralline red algae and sponges, which, along with micritic cements, comprise the bulk volume of the reef. The most abundant alga and primary reef constructor is *Archaeolithothamnium*. Also present are *Lithoporella, Mesophyllum,* and possibly *Lithothamnium, Tenarea,* and *Lithophyllum* (E. Praeger, pers. comm., 1991).

Crustose coralline red algae are common inhabitants of reef and forereef environments in both Tertiary and Recent buildups (Adey and MacIntyre, 1973; Wray, 1977; Ghose, 1977). In the Salt Mountain, they occur as both thick (5 mm), but primarily thin (1-2 mm) crusts. According to Steneck (1986) thin crusts are indicative of comparatively greater water depths and slower growth rates relative to thicker coralline crusts. The depth range of overlap of thin and thick crustose corallines in modern reefs ranges from 5-20m (Steneck, 1986, fig. 4).

The dominant Salt Mountain red alga, *Archaeolithothamnium*, is today a tropical to subtropical genus that is most abundant in relatively deep waters (60-80 meters; Minnery, 1990), although it has a broad bathymetric distribution and certainly reached into shallower water during the Paleogene. The genus, for example, constructed rock-forming abundances of rhodoliths around Early Oligocene fringing coral reefs in Georgia and Florida (Manker and Carter, 1987; Carter *et al.*, 1995).

The Salt Mountain sponge fauna should prove to be especially informative when it

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PLATE 3

Some common sponge body fossils of the Salt Mountain Limestone, from Biofacies 3. Specimens deposited at Okaloosa-Walton Community College.

Figures
1. OW 00103. Size: 8.5 cm by 5.6 cm.
2. OW 00107. Size: 2.7 cm by 2.9 cm.
3. OW 00108. Size: 5.4 cm by 4.4 cm.
4. OW 00109. Size: 3.2 cm (width) by 2.6 cm (height).
5. OW 00106. Two, narrow tubular sponges. Size: 11.7 cm by 3.2 cm (top).
6. OW 00101. Polished cross-section of large, tubular sponge. Size: 6.8cm by 5.3 cm.
7. OW 00105. Size: 7.4 cm by 6.0 cm.
8. OW 00110. Size: 11.7 cm by 4.2 cm.
9. OW 00111. Size: 5.4 cm by 2.9 cm.
10. OW 00112. Size: 5.9 cm by 2.9 cm.
11. OW 00104. Size: 9.8 cm by 5.7 cm.
12. OW 00102. Laminar, encrusting sponge. Size: 13.6 cm by 5.9 cm.

PLATE 3

is described. At least 15 distinct morphotypes can be consistently identified among the larger sponge body fossils (Plate 3). The size of sponge body fossils ranges from small, 2 cm oblong buds to large, vase- or barrel-shaped forms reaching uncertain size (perhaps from 50 cm to 1 meter in length). Most are 2 to 10 cm in length, with a variety of growth forms (conical, tubular, anasthomosing, laminar-encrusting, etc.). J. Keith Rigby (pers. comm., 1990) recognized two species of hexactinellid in the Salt Mountain: one dictyid or lychniskid, with a cylindrical body and net-like skeleton; and one lyssakid, with a more irregular skeleton and spicules irregularly oriented and spaced within the skeleton.

Very little is currently known of Tertiary sponge faunas, but those described usually consist of several Cretaceous "holdover" species (Weidenmayer, 1980, p.84; Finks, 1986). It is expected that many of the Salt Mountain taxa will also have strong Mesozoic affinities. In the southeastern United States, Tertiary sponges have rarely been reported. Rigby and Smith (1992) describe microscleres from choristic demosponge *Geodia* from the Paleocene (Danian) Porters Creek Formation of southwestern Alabama, and undescribed hexactinellids have recently been discovered in the Eocene Shubuta Marl near Perdue Hill, Alabama. But the largest fauna known to date is the Middle Eocene Castle Hayne Limestone of North Carolina. The Castle Hayne has a large sponge fauna (17 species) occurring in two facies: one dominated by hexactinellids and lithonine Calcarea, and a shallower facies with dominant demosponges (choristids and plinthosellid lithistids) and fewer hexactinellids (Finks, 1986; Rigby, 1981). These sponges, however, did not construct a reef, nor are they associated with larger foraminifera, coralline algae, or corals. The Castle Hayne was evidently a temperate water carbonate.

X. SEQUENCE STRATIGRAPHY AND REEF GROWTH

As pointed out by Fluegeman (this volume), only the mid- to upper portion of the Salt Mountain may correlate with the lower portion of the "*Ostrea thirsae* beds" member of the Nanafalia Formation (a transgressive systems tract). The lower 20 meters or so of the Salt Mountain may correlate with the non-marine, incised-valley fill, Gravel Creek Sand Member (the lowest member) of the Nanafalia Formation (a lowstand systems tract).

This correlation is important with regard to the depositional environment of the Salt Mountain. It would imply that the Salt Mountain began as a low-stand carbonate during Gravel Creek time–early TP2.1 cycle (Mancini and Tew, 1991; Baum and Vail, 1988, fig. 13), and confirm a shallow neritic origin for the Salt Mountain. The reef core of the Salt Mountain would then have been deposited as a transgressive carbonate, probably equivalent to the lower portion of the "*Ostrea thirsae* beds" of the Nanafalia Formation.

If this correlation is correct, the Salt Mountain could represent no more than 2 million years of deposition (*i.e.*, from the beginning of cycle TA2.1 at 58.5 Ma, to the development of the condensed section at 56.5 MA; Haq *et al.*, 1988), and probably much less–particularly if the Salt Mountain is entirely younger than the Gravel Creek Sand. Eustatic sea level rise during the TA2.1 third order cycle (late Thanetian) was large–perhaps up to 125 meters or more (Haq *et al.*, 1988, fig. 14). A conservative estimate of 100 meters rise in 2 million years is equivalent to an average rate of rise of 50 mm per 1000 years, or 50 Bubnoffs (1 Bubnoff = 1mm/1000 years; Kendall and Schlager, 1981). This is well within the range of typical third order sea level cycles (10-100 Bubnoffs; Kendall and Schlager, 1981). Assuming a maximum duration of the reef of 2 million years, constant deposition throughout the TA2.1 cycle, and given a thickness of approximately 40 meters (130 feet) at the type section, a minimum accumulation rate for the Salt Mountain would be 20 mm per 1000 years, or 20 Bubnoffs.

What, then, was the fate of the Salt Mountain reef? From these estimates, the reef would not have been able to keep up with sea level rise. But according to Schlager (1991), typical third-order sea level cycles are too slow to drown most healthy reefs (accretion rates of most Holocene reefs range from approx.1000-10,000 Bubnoffs, depending on depth;

Schlager, 1992). The actual growth rate of the Salt Mountain was certainly much greater than 20 Bubnoffs. There are no evident unconformities at the type section (Toulmin, 1955), nor mineralized hardgrounds. There are perhaps two shallowing-upwards depositional cycles (Bryan, 1991) and massive corals are found at the top of the formation. The reef appears to have easily kept pace with sea level rise.

Schlager (1992) mentions the common occurrence of echinoderm-rich grainstone facies with drowning events, and the fact that many drowning "unconformities" do not represent significant stratigraphic hiatuses. The Salt Mountain does have an echinoid-rich (but muddy) facies at the top of the type section, but why such facies should be associated with drowning is unclear (perhaps incipient drowning and hardground development favor an increased recruitment of the epifaunal regular echinoids). While the reef may have drowned from an abrupt deepening, it is more likely that the Salt Mountain coral-algal-sponge reef was simply overwhelmed by siliciclastic influx.

Although difficult to see in outcrop, the Salt Mountain is overlain by over 21 meters (70 feet) of "Wilcox clay" (possibly of the Nanafalia Formation; Causey and Newton, 1972). Toulmin (1962, 1967) describes this lithology as: "Clay, light gray to medium light gray, weathers pale

TABLE 1. Sample Descriptions from Grid 21, Salt Mountain Limestone. Listed are the volumetrically dominant components. Other biochems are common. All "algae" in descriptions refer to coralline red algae, predominantly but not exclusively *Archaeolithothamnium*.

Sample	*Description*
1a	Sponge-algal boundstone. 55 mm x 15/30 mm hexactinellid encrusted by coralline red algae.
1b	Algal boundstone (possibly with encrusting sponge or stromatolites) overlain by echinoderm-bryozoan-algal biomicrite; some coral. The biomicritic matrix appears to fill cavities or borings within the algal boundstone.
1c	Bryozoan-algal biomicrite. Some coral, echinoid spines.
2a	Bryozoan-algal biomicrite. Some encrusting foraminifera with algae; minor sponge, coral, echinoid spines.
2b	Sponge-algal boundstone/bryozoan biomicrite. Rare coral, discocyclinids.
2c	Coral framestone (*Stylophora ponderosa*, partially overlying bryozoan biomicrite).
3a	Algal boundstone, overlying bryozoan-algal biomicrite.
4a	Sponge-algal boundstone. Some echinoid spines.
4b	Sponge-algal boundstone, with bryozoan-algal biomicrite.
4c	Coral-algal-sponge boundstone, with bivalve boring (*Lithophaga*) and bryozoan-algal biomicrite matrix. Some echinoderm spines.
5a	Sponge-algal boundstone.
6a	Coral-sponge-algal boundstone, with bryozoan biomicrite matrix.
6b	Sponge-algal boundstone. Rare discocyclinids.
7a	Sponge-algal boundstone.
7b	Sponge-algal boundstone, with bryozoan biomicrite matrix. Encrusting foraminifera, mollusc and/or brachiopod fragments.
8a	Sponge-algal boundstone.
8b	Sponge boundstone.
9a	Sponge-algal boundstone, with *Lithophaga* borings.
10a	Bryozoan biomicrite. Possible algal boundstone, sponge.
12a	Bryozoan biomicrite.
14a	Sponge-algal boundstone.
15a	Algal boundstone, with bryozoan biomicrite.

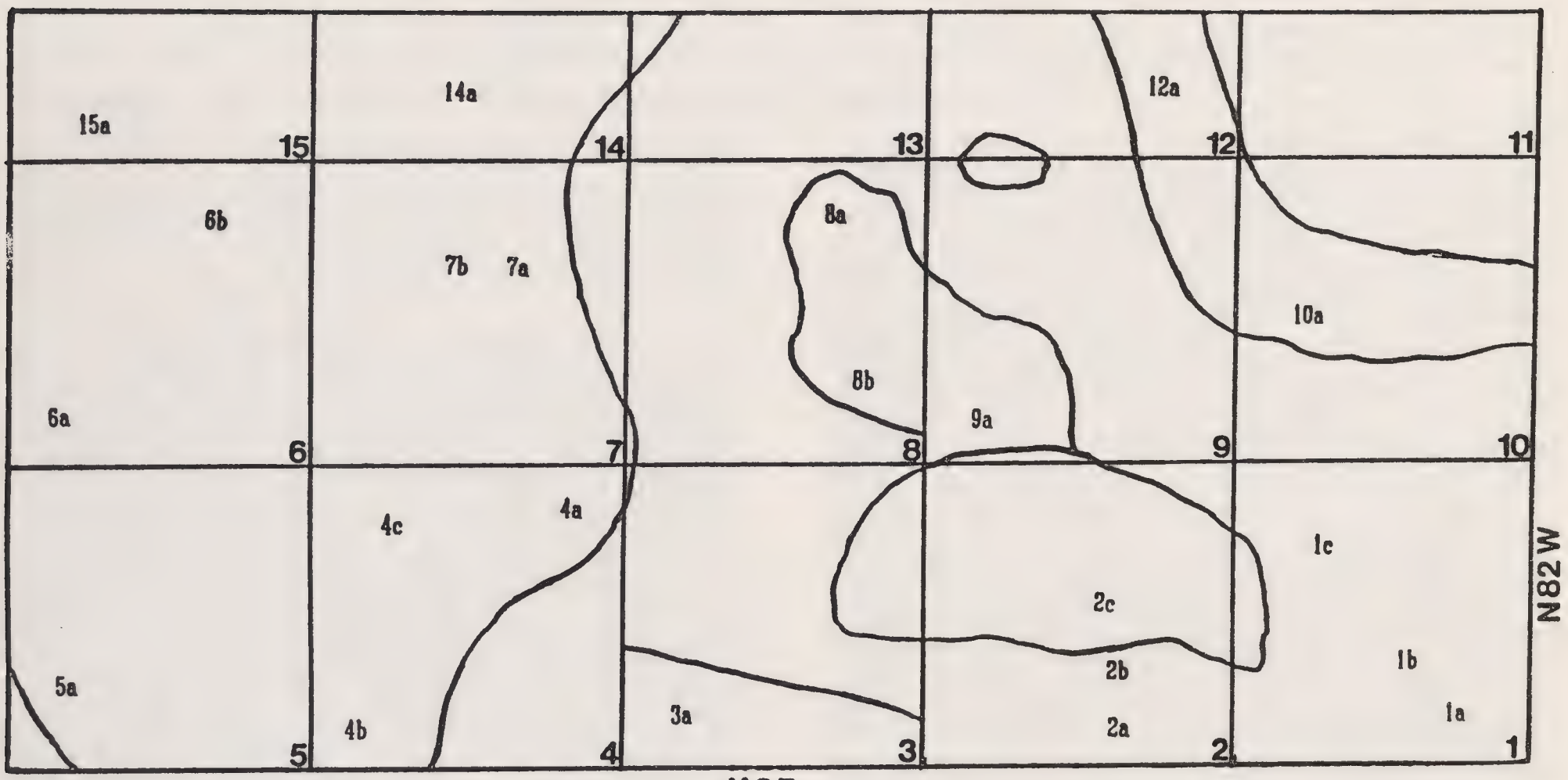
Text-figure 4. *In situ* colony of *Stylophora ponderosa* at sampling station number 21 (see Text- figures 3, 5).

to dark yellowish-orange, thin-bedded to massive, very finely sandy, glauconitic, micaceous, subconchoidal fracture; contains some thin partings of fine-grained sand from which flakes of limonite weather; includes in the lower part a 1-foot layer of fine- to coarse-grained very glauconitic sand. The lower part of the bed near the contact with the Salt Mountain Limestone is pale yellowish brown massive blocky clay. The change from limestone to clay is abrupt, but the contact is apparently conformable." Toulmin (1955, p.219) also indicates that, "Downdip in southwestern Alabama near the coast the undifferentiated Wilcox above the Salt Mountain limestone consists of dark gray micaceous carbonaceous shale with some lignite steaks and some beds of gray and brown hard marl and brown claystone."

It is assumed then that the demise of the reef was caused by siliciclastic influx from the prograding Holly Springs Delta System. These Wilcox Group siliciclastics overwhelmed carbonate production and buried the reef.

XII. THE SALT MOUNTAIN LIMESTONE AND THE POST-CRETACEOUS RECOVERY OF PHOTIC-ZONE REEFS

There is a growing literature on the recovery of reef communities following Phanerozoic mass extinction events (*e.g.*, Newell, 1971; Heckel, 1974; Sheehan, 1985; Talent, 1988; Copper, 1988, 1989, 1994; Kuznetsov, 1990; Flugel and Flugel-Kahler, 1992; Kauffman and Fagerstrom, 1993; Wood, 1993, 1995). And there is a general consensus that during mass extinctions, shallow-water tropical reef communities suffer disproportionately relative to other benthic communities. Reefs typically are the first benthic communities to suffer from the extinction event, experience the greatest diversity loss relative to other marine benthos, and delay recovery for 2 to 10 m.y. or more after the extinction (temperate water benthic communities may rebound within 1-2 m.y.). But



Text-figure 5. Meter sampling grid with subsamples taken at sample station number 21 (see Text-figure 3). See Table 1 and text for discussion.

questions remain over the recovery phase: Are the initial post-extinction reefs trophically similar to pre-extinction reef communities? Does community recovery show any ecological succession? Do stress-tolerant, eurytopic taxa initiate reef recovery (perhaps in an offshore to onshore move or as Lazarus immigrants), creating novel (temporary or permanent) post-extinction reefs?

Despite this interest, however, there is perhaps the least documentation of reefs immediately following the best-studied mass-extinction, the Cretaceous-Tertiary (K-T) event (Copper, 1994a). After the terminal Cretaceous loss of rudist-coral reefs, diverse scleractinian-dominated reefs were not widespread until the mid-late Eocene. Paleocene photic-zone reefs are indeed rare and insufficiently documented, prompting Copper (1989) to ask, "Why did it take nearly 10 million years for reefs to begin even a modest recovery to patch reef size following the...end-Cretaceous (extinction)...when corals, sponges, and other metazoans were available as the pioneers for new reef ecosystems?" During the Danian Stage of the Paleocene, there were evidently no significant oligotrophic adaptations nor photic-zone reef development anywhere. Photic-zone carbonates were instead dominated by coralline red algae, bryozoa, brachiopods, and oyster bioherms. Conspicuously absent at this time are the larger benthic foraminifera (LBF), which were common inhabitants of both Late Cretaceous and Late Paleocene to Recent reef facies.

Oligotrophic adaptations are evident, however, by the Thanetian Stage of the Paleocene (plankton Zone P4, 8 m.y. after the K-T boundary) in the form of photosymbiont-hosting, K-strategist planktonic and LBF (Hallock *et al.*, 1991; Hottinger, 1987). Limited hermatypic coral associations developed in the Late Paleocene, but these reefs were generally small, low-diversity coral-algal patch reefs. Most Thanetian carbonate platforms such as those of Libya (Terry and Williams, 1969), Oman (Racz, 1979), Egypt (Kuss and Leppig, 1989), India (Ghose, 1976,1977), and offshore Brazil (Carozzi, 1989) were large foram- and/or coralline algal-dominated ramps (Mresah, 1993). True reef-rimmed shelf margins may have been entirely absent at this time (J. Kuss, 1990, pers. comm.). Mresah (1993) suggests that larger foraminifera, particularly nummulitids, temporarily occupied the vacant ecologic niches left by scleractinian corals after the K-T event.

The Salt Mountain reef (Thanetian, Zone P4) was constructed by coralline algae and sponges (primarily hexactinellids), with common but low diversity scleractinians and abundant discocyclinid LBF, bryozoa, brachiopods, endolithic bivalves, and cidaroid echinoids. The constructional dominance of coralline algae and sponges would seem to indicate that scleractinians had still not yet established their role as primary reef framestone builders, which they would display in photic-zone reefs from the Eocene to the present. The abundance of hexactinellid sponges in the Salt Mountain may be especially significant. Heckel (1974) suggested that sponges were major reef builders only in the absence of other groups, or when environmental conditions were unfavorable for these groups. Likewise, Copper (1989) noted the persistence of algae and sponges in Phanerozoic reef development, with corals only present during optimal conditions. The siliceous hexactinellids are exclusive K-strategists, requiring stable environments, but are bathymetrically tolerant. They reached their greatest diversity in the Late Cretaceous and were common reef/mound constructors in the Jurassic (Rigby, 1987; Mehl, 1992). Their presence in the Salt Mountain suggests a temporary role as early post-Cretaceous photic-zone reef constructors prior to the full recovery of scleractinian-dominated reefs in the later Paleogene.

XII. ACKNOWLEDGMENTS

Special thanks are extended to two student research assistants from Okaloosa-Walton Community College. They assisted in field collecting and laboratory preparations, and both made important new discoveries of Salt Mountain fauna. Mr. Paul S. Kline, now a geology student at the University of Alabama, Tuscaloosa, assisted in the summer of 1995. And Ms. Stephanie Schroeder, of Eglin Air Force Base, Florida, assisted in the summer of 1996. Roger Portell (Florida Museum of Natural History) loaned topotypes of Salt Mountain larger foraminifera collected by Lyman Toulmin.

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PART II
SMALLER BENTHIC FORAMINIFERAL PALEOECOLOGY

RICHARD H. FLUEGEMAN, JR.

I. INTRODUCTION

A recent paper by Bryan (1991) examined the biofacies within the late Paleocene age Salt Mountain Limestone of Alabama and reconstructed the paleoecology of the megafossil assemblages within the unit. The Salt Mountain is a 37 meter thick reefal limestone known principally from the subsurface and from its single outcrop in Clarke County, Alabama. Bryan's work was the first detailed paleoecologic examination of the faunas of the Salt Mountain. Especially significant in this study was the recognition of sponges as an important constituent of the Salt Mountain reef communities. This association is considered unique among the poorly known Paleocene reefs worldwide. Considering the limited knowledge of Paleocene reefs, Bryan (1991) has provided valuable insight into the survival and recovery of reef communities following the Cretaceous-Paleogene extinction.

Placing these results within a proper sequence stratigraphic framework would further enhance the understanding of early Paleogene reefs and their relationship to fluctuating sea-level. Although sequence stratigraphy of outcropping Paleogene sediments has been studied in the eastern Gulf Coastal Plain of the United States (Baum and Vail, 1988; Mancini and Tew, 1991) the Salt Mountain Limestone was not included. Carbonate depositional systems respond differently to fluctuating sea-level than do siliciclastic systems (Sarg, 1988; Schlager, 1992) and a simple comparison of the Salt Mountain section to those siliciclastic sections previously studied updip may be misleading.

Studies of benthic foraminiferal paleoecology provides a tool to help place the Salt Mountain Limestone within a sequence stratigraphic framework by reconstructing the sea-level history of the unit. Briskin and Fluegeman (1990) studied benthic foraminiferal assemblages from the Paleocene of the eastern Gulf Coastal Plain and were able to place paleoecologic and paleobathymetric estimates on identified sequences. Additionally, their study of assemblages identified some smaller scale fluctuations of sea-level within some of the sequences. The principles on which Briskin and Fluegeman based their study were the understanding that the distribution of benthic foraminiferal assemblages are controlled by water mass characteristics (Streeter, 1973; Lohmann, 1978) and are not affected by substrate type (Culver and Buzas, 1982). While not a measure of absolute bathymetry, benthic foraminiferal assemblages do reflect paleoecologic conditions, which may change with either water depth or distance from the shoreline. In either case, changes in assemblages through time should reflect a change in relative sea-level. The independence from substrate type enables a comparison from carbonate to siliciclastic depositional settings where the respective sedimentological responses to fluctuations in relative sea-level are likely to be quite different.

II. AGE AND CORRELATION

Tappan and Loeblich (1957) studied planktonic foraminifera from the Salt Mountain and identified it as a Paleocene unit assignable to the *Planorotalites pseudomenardii* Zone (Zone P4). The work of Wind (1974) and Siesser (1983) identified calcareous nannofossils from the middle and upper portion of the Salt Mountain and assigned the formation to the *Discoaster muehleri* Zone (Zone NP7). Both of the biostratigraphic assignments are consistent with a late Paleocene age and suggest a correlation with the "*Ostrea thirsae* beds" of the Nanafalia Formation of the Paleocene outcrop belt.

This correlation may be an oversimplification. While both units contain calcareous nannofossils of zone NP7, the bulk of the "*Ostrea thirsae* beds" are actually within zone NP8 (Gibson *et al.*, 1982). Additionally, the zone NP7 nannofossils from the Salt Mountain are from near the middle and top of the section suggesting that the Salt Mountain may be at least in part correlative with the non-marine Gravel Creek Member of the Nanafalia Formation. No nannofossils have been identified from the lower 20 m of the Salt

Mountain.

Other biostratigraphic work has been done on the Salt Mountain and the "*Ostrea thirsae* beds." Both units are in planktonic foraminiferal zone P4 but this is a broad zone representing more than 3 million years (Berggren *et al.*, 1995). A revised planktonic foraminiferal biozonation presented in Berggren *et al.*(1995) divides Zone P4 into three subzones. The "*Ostrea thirsae* beds" are placed in subzone P4c based on the presence of both *Globanomalina pseudomenardii* and *Acarinina soldadoensis*. Planktonic foraminifera have only been collected from the lower part of the Salt Mountain and *G. pseudomenardii* is the only biostratigraphically important species present. The presence of *Globoanomalina pseudomenardii* and the absence of *Acarinina soldadoensis* suggests that the lower part of the Salt Mountain should be assigned to subzone P4b. Also absent from the Salt Mountain Limestone is the distinctive benthic foraminifer *Discorbis washburni*. This fossil is a characteristic element of the benthic foraminiferal fauna of the "*Ostrea thirsae* beds" and defines the *Discorbis washburni* total range zone of Fluegeman *et al.* (1990).

The above biostratigraphic data suggest that the Salt Mountain Limestone may correlate in part with the "*Ostrea thirsae* beds" of the Nanafalia Formation but that a significant portion (as much as 20 meters) of the Salt Mountain Limestone may correlate with the underlying Gravel Creek Member of the Nanafalia Formation.

III. BENTHIC FORAMINIFERA

Benthic foraminifera were first described from the Salt Mountain Limestone by Vaughan (1936). He described the larger foraminifera *Discocyclina weaveri* and *Pseudophragmina stephensoni* from the Salt Mountain. Toulmin (1941) described and illustrated the entire foraminiferal fauna collected from the base of the Salt Mountain. In addition to the larger foraminifera already described, he identified a diverse assemblage of smaller foraminifera.

The presence of species of *Discocyclina* and *Pseudophragmina* suggests an affinity with the Tethyan fauna described by Berggren (1974) from the Sirte Basin of Libya and Mali. After evaluating the entire fauna reported by Toulmin (1941) however, Berggren and Aubert (1975) concluded that the Salt Mountain benthic foraminiferal fauna was a typical assemblage of the cosmopolitan "Midway Fauna." Briskin and Fluegeman (1990) did use Salt Mountain benthic foraminiferal data in their study of assemblages and they did identify a *Discocyclina-Pseudophragmina* assemblage as characteristic of reef environments. They recognized this assemblage as an "overprinted" assemblage occurring in the same samples with a typical Midway association. Because of the isolated occurrence of the Salt Mountain assemblages and the uncertainty of their correlation, Briskin and Fluegeman (1990) did not use the Salt Mountain data in constructing their paleontologic sea-level curve.

IV. METHODS OF STUDY

Samples were collected at 1 m intervals through the 37 meters of Salt Mountain Limestone at the type locality. In the laboratory, thin sections were made of all samples and examined to determine rock type and foraminiferal constituents. Samples were assigned to one of the four biofacies identified by Bryan (1991). Disaggregation was attempted on a portion of each sample. The samples were dried for 24 hours at 100 degrees Celsius. They were then soaked in de-ionized water for 24 hours. The samples were then wet sieved and dried for an additional 24 hours. The resulting washed material was then examined under a binocular microscope and individual foraminifera were identified. Because of the degree of lithification, the washing procedure did not produce complete disaggregation in any of the samples. Some washed material was obtained from all samples with the exception of the boundstones. Foraminifera were picked and identified using the taxonomy of Toulmin (1941), as modified by Berggren and Aubert (1975). The obtained foraminifera were censused and each sample was assigned to one of the paleoecologic assemblages identified by Briskin and Fluegeman (1990).

V. BENTHIC FORAMINIFERAL PALEOECOLOGY

Foraminifera were identified from throughout the Salt Mountain Limestone. Most of the faunas could be assigned to one of the assemblages identified by Briskin and Fluegeman (1990). In the case of the boundstones, an insignificant wash necessitated thin section study of the foraminifera. In these samples, the most conspicuous components of the fauna were identified. Examination of the literature on benthic foraminifera enabled assignment of these samples to paleoecologic assemblages.

The lower 3 meters of the Salt Mountain Limestone consists of a foraminiferal-bryozoan-algal biomicrite (Biofacies 1 of Bryan, 1991). It is from this unit that Toulmin (1941) collected his foraminiferal fauna. Samples collected from this interval in this study had the most complete disaggregation and thus the best foraminiferal assemblages were collected here. Benthic foraminifera collected from the lower meter of this unit are assignable to the *Pulsiphonina-Anomalinoides* assemblage of Briskin and Fluegeman (1990). This assemblage is characterized by an abundance of the species *Pulsiphonina prima* and *Anomalinoides acuta*. Other abundant species associated with this assemblage in the Salt Mountain Limestone include *Marsonella oxycona, Discocyclina weaveri, Pseudophragmina stephensoni, Alabamina westraliensis,* and *Nonionella insecta*. This assemblage has been identified from a number of localities worldwide (Berggren and Aubert, 1975) and it has been assigned to a variety of bathymetric ranges. Briskin and Fluegeman (1990) considered this assemblage to represent those paleoecologic conditions found at from 15-30 meters of depth.

The next meter contains benthic foraminifera assignable to the *Cibicidoides-Anomalinoides* assemblage of Briskin and Fluegeman (1990). This assemblage is characterized by an abundance of *Cibicidoides alleni* and *Anomalinoides midwayensis* associated with a diverse foraminiferal fauna including, in the Salt Mountain Limestone, *Discocyclina weaveri* and *Pseudophragmina stephensoni*. This assemblage is a common association within the Midway fauna throughout the world (Berggren and Aubert, 1975) and is generally considered to represent water depth of 5 - 10 meters. Briskin and Fluegeman (1990) concurred and considered this assemblage to represent inner neritic conditions. The occurrence of this assemblage in the Salt Mountain Limestone represents a relative fall in sea-level from the conditions of the lower part of this unit.

The upper part of the lower unit of the Salt Mountain contains an assemblage assignable to the *Lenticulina-Anomalinoides* assemblage of Briskin and Fluegeman (1990). This assemblage is characterized by the abundance of *Lenticulina midwayensis* and *Anomalinoides umbonifera* and a general low diversity of benthic foraminifera. *Discocyclina weaveri* and *Pseudophragmina stephensoni* are present in this assemblage in the Salt Mountain. The *Lenticulina-Anomalinoides* assemblage was first recognized in the Aquia Formation of Maryland and Virginia by Nogan (1964). He interpreted this assemblage to represent water depth of less than 5 meters. Briskin and Fluegeman (1990) considered the *Lenticulina-Anomalinoides* assemblage to indicate littoral, subtidal conditions. This interpretation is accepted here for the upper part of this unit of the Salt Mountain Limestone.

The next 7 meters of the Salt Mountain Limestone consist of a sponge-coral biomicrite. This is biofacies 3 of Bryan (1991). The lithified nature of the rocks in this interval prevented the collection of foraminiferal assemblages by washing. Thin section studies reveal numerous individuals of *Discocyclina weaveri* and *Pseudophragmina stephensoni*. This interval is assigned to the *Discocylclina-Pseudophragmina* assemblage of Briskin and Fluegeman (1990). They considered this assemblage to be associated with reef environments. In the case of the Salt Mountain Limestone, the *Discocylina-Pseudophragmina* assemblage is restricted in use to the main body of the reef. The few foraminifera obtained from washings from this interval are mostly individuals of *Lenticulina toddae*. This association of the *Lenticulina-Anomalinoides* assemblage suggests water depth of less than 5

meters for the *Discocylina-Pseudophragmina* assemblage. This is consistent with the bathymetric estimates of the lower unit and indicates a stabilization of reef development.

In the next 10 meters of the Salt Mountain Limestone, the lithology is again assignable to Biofacies 1 of Bryan (1991). Benthic foraminifera collected from washings are assignable to the *Pulsiphonina-Anomalinoides* assemblage. *Discocyclina weaveri* and P*seudophragmina stephensoni* are also common constituents of the fauna. Both the lithology and the benthic foraminifera indicate a rise in relative sea-level.

Overlying this unit is a coral biomicrite. This unit is identified by Bryan (1991) as Biofacies 2. The unit as measured in this study is 8 meters thick. Foraminifera obtained from washings of this interval are robust individuals of *Anomalinoides umbonifera, Lenticulina midwayensis*, and *Lenticulina toddae*. Numerous individuals of *Lenticulina* sp. are also visible in thin section. Specimens of D*iscocyclina weaveri* and *Pseudophragmina stephensoni* are rare in this interval with only two isolated tests seen in thin section. The above association suggests assignment of this interval to the *Lenticulina-Anomalinoides* assemblage. The paleoecologic conditions implied by this assemblage are consistent with the interpretation of this biofacies as a low energy thicket near the main reef buildup (Bryan, 1991) and indicates a fall in relative sea-level.

Overlying this interval is a recurrence of Biofacies 3. The unit is 7 meters thick and is assigned to the *Discocyclina-Pseudophragmina* assemblage. This indicates the development of reef conditions and a further fall in relative sea-level.

The upper 2 meters of the Salt Mountain Limestone consists of a coral-echinoderm biomicrite. This is Biofacies 4 of Bryan (1991). The foraminifera collected from this interval indicate assignment to the *Pulsiphonina-Anomalinoides* assemblage. The paleoecologic conditions implied by the presence of this assemblage represent a rise in relative sea-level, and thus deeper water conditions than either Biofacies 2 or 3. This interpretation differs from that of Bryan (1991) who interpreted the coral-echinoderm facies to be a shallow water backreef deposit. The distribution of the benthic foraminiferal assemblages and the biofacies of Bryan (1991) are shown in Text-figure 1.

VI. DISCUSSION: FORAMINFERAL PALEOECOLOGY AND SEQUENCE STRATIGRAPHY OF THE SALT MOUNTAIN LIMESTONE

As discussed previously, the Salt Mountain Limestone does not fit into most of the sequence stratigraphic interpretations of the Paleogene of the eastern Gulf Coastal Plain. The fact that the sequence models developed for the region deal mostly with clastics is certainly a part of this difficulty but the greatest problem has been the lack of a precise correlation with the sections of the Paleocene outcrop belt to the North. The published planktonic foraminiferal age (P4) for the entire Salt Mountain Limestone and calcareous nannofossil age (NP7) for the upper half of the formation suggest an age no younger than the lower part of the "*Ostrea thirsae* beds" of the Nanafalia Formation. When the revised planktonic foraminiferal biostratigraphy of Berggren *et al.* (1995) is considered, the lower part of the Salt Mountain may be older than the entire "*Ostrea thirsae* beds." These plus the presence of the benthic foraminiferan *Alabamina westraliensis* and the absence of both *Discorbis washburni* and *Nonion graniferum* make a strong argument that the Salt Mountain is older than the *Discorbis washburni* benthic foraminifera zone. If this is the case, the Salt Mountain Limestone is a correlative of the Gravel Creek Member of the Nanafalia Formation, the lowstand deposits of Cycle TA 2.1 of Haq *et al.*(1987).

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Text-figure 1. Section of the Salt Mountain Limestone showing the distribution of benthic foraminiferal assemblages and their relationship to biofacies of Bryan (1991). Abbreviations: L-A = *Lenticulina-Anomalinoides* assemblage, C-A = *Cibicidoides-Anomalinoides* assemblage, P-A = *Pulsiphonina-Anomalinoides* assemblage, D-P = *Discocyclina-Pseudophragmina* assemblage.

m	Lithology	Benthic Foraminifera	Biofacies
36		P – A	4
34		D – P	3
32			
30			
28		L – A	2
26			
24			
22			
20		P – A	1
18			
16			
14			
12			
10		D – P	3
8			
6			
4			
2		L – A	1
		C – A	
		P – A	

Lowstand carbonate wedges were defined and classified by Sarg (1988). Further work on carbonate sequence stratigraphy by Schlager (1992) clarified the characteristics of carbonate sediments deposited during lowstand conditions. Of particular interest here is the lowstand wedge developed during long (durations in millions of years) sea-level cycles and in conjunction with gentle depositional slopes. The depositional setting of Salt Mountain Limestone is consistent with these conditions. The Salt Mountain formed during Cycle TA 2.1 of Haq *et al.*(1987). They consider this cycle to have had a duration of 3.5 ma. The long sea level cycle plus the broad nature of the shelf in the eastern Gulf of Mexico during Paleocene time would both be conducive to the development of a lowstand carbonate wedge provided the physical, chemical, and biological conditions necessary for carbonate sediment development are met.

Is it reasonable to associate a lowstand carbonate wedge with a siliciclastic sequence? The models of Sarg (1988) and Schlager (1992) deal exclusively with carbonate platforms and genetically linking the Salt Mountain Limestone to the Gravel Creek Member of Nanafalia Formation may not be appropriate. The Salt Mountain could be a lowstand carbonate wedge associated with the northern margin of the Suwannee Channel. During much of Paleogene time, this margin was the site of reef buildups (Chen, 1965). Additionally, both the Cedar Key and Oldsmar Limestones of Paleocene age in the Florida subsurface are reefal limestones (Levin, 1957; Chen, 1965) and are associated with the Suwannee Channel margin. Similarities have also been noted between the Salt Mountain Limestone and the Paleocene Clayton Formation of southeastern Alabama and southwestern Georgia by Bryan (1993). The above works document the presence of a well developed carbonate shelf during Paleocene time in close proximity to the outcrop of the Salt Mountain Limestone. The actual connection between the Salt Mountain and the carbonate shelf is a bit tenuous however, due to the lack of detailed subsurface information in the area.

Can lowstand carbonates develop without a carbonate shelf in close proximity? Rezak *et al.*(1985) document several carbonate banks in the northwestern Gulf of Mexico. These banks developed on top of salt diapirs on an otherwise clastic shelf. Bryan (1991) used these reefs as a model for the Salt Mountain Limestone. These reefs were at their maximum development during the last glacial maximum, a sea-level lowstand. If the Salt Mountain developed at lowstand, there should be some evidence of drowning with rising sea-level. The succession of benthic foraminiferal assemblages is consistent with this pattern. Further, Schlager (1992) identifies "encrinite" lithologies capping drowned lowstand reef sequences. While the upper lithology at Salt Mountain is not an echinoderm grainstone, many of the grains are rounded and the rock is well sorted. This with the presence of the *Pulsiphonina-Anomalinoides* assemblage indicate increasing water depth and rising relative sea-level.

In summary, benthic foraminifera from the Salt Mountain Limestone record a pattern of fluctuating sea-level similar to that suggested by Bryan (1991) in his study of biofacies. Further, the fluctuation in relative sea-level recorded in the lower part of the Salt Mountain Limestone may be the sea-level cycle equivalent to the Gravel Creek Member of the Nanafalia Formation suggested by Briskin and Fluegeman (1990). This cycle was inferred by a study of sea-level periodicity in the Paleocene and was thought to have occurred during a long lowstand phase.

PART III
LARGER FORAMINIFERA

JONATHAN R. BRYAN

I. INTRODUCTION

Only two species of larger benthic foraminifera (LBF) have been recognized from the Salt Mountain Limestone, but the stratigraphic, biogeographic, and ecologic significance of these taxa make them worthy of some discussion.

II. SYSTEMATIC PALEONTOLOGY

The frequent nomenclatorial changes that plague LBF generally have affected the Salt Mountain species as well. Vaughan (1936) first described two species of *Discocyclina* from the Salt Mountain, *D. blanpiedi* and *D. cookei*, distinguished by test size, test shape, size of the embryonic chambers, and features of the equatorial chambers. Cole (1959, 1969) later synonymized these two species as follows:

Discocyclina (Discocyclina) weaveri Vaughan, 1929

(= *Discocyclina blanpiedi* Vaughan, 1936)

Pseudophragmina (Athecocyclina) stephensoni (Vaughan), 1929

(= *Discocyclina cookei* Vaughan, 1936)

Classifications of the discocyclinids vary. I have followed Cole (1964, 1969) and Loeblich and Tappan (1988). Synonymies are not complete, but list original and other important or recent references.

Order FORAMINIFERIDA
Eichwald, 1830
Suborder ROTALIINA Delage and Herouard, 1896
Family DISCOCYCLINIDAE
Galloway, 1928
Genus DISCOCYCLINA Gumbel, 1870
DISCOCYCLINA (DISCOCYCLINA) WEAVERI
Vaughan, 1929
Plate 1, figure 1

Discocyclina (Discocyclina) weaveri VAUGHAN, 1929, pl. 1, figs.1,2.

Discocyclina blanpiedi VAUGHAN, 1936, pl.41, figs.1-7 (Salt Mountain Limestone).

Discocyclina (Discocyclina) weaveri Vaughan. COLE, 1959, pl.33, figs.3-5 (full synonymy p. 384).

Remarks: According to Vaughan's original description, *D. weaveri* "possesses an embryonic apparatus in which the second chamber almost entirely surrounds the first and the first two chambers are nearly surrounded by a ring of chambers larger than the succeeding equatorial chambers." In the 1936 description of "*D. blanpiedi*" from the Salt Mountain, Vaughan notes that the deuteroconch only partly embraces the protoconch. Cole (1959) points out that the original specimen illustrated by Vaughan (1929) was obliquely oriented, giving only the appearance of a eulepidine embryonic apparatus. The deuteroconch is distinctly reiniform. The equatorial chambers are distinct, each with well-defined walls, yet arranged in annuli, and appear subrounded to oblong, but usually retaining the hexagonal shape.

Family ASTEROCYCLINIDAE
Bronnimann, 1951
Genus PSEUDOPHRAGMINA
H.Douville, 1923
PSEUDOPHRAGMINA (ATHECOCYCLINA) STEPHENSONI (Vaughan, 1929)
Plate 1, figure 2

Discocyclina stephensoni VAUGHAN, 1929, pl. 6, figs. 1-4.

Discocyclina cookei VAUGHAN, 1936, pl. 42, figs. 1-6 (Salt Mountain Limestone).

Pseudophragmina (Athecocyclina) stephensoni (Vaughan).COLE,1953, pl.2, figs.4-11 (subsurface of Georgia).

Pseudophragmina (Athecocyclina) stephensoni (Vaughan).COLE, 1959, pl.32, figs.1-4 (full synonymy p.386).

Pseudophragmina (Athecocyclina) cookei (Vaughan). COLE, 1964, fig. 588,3.

Pseudophragmina (Athecocyclina) stephensoni (Vaughan). COLE, 1969, pl.6, figs.1,2.

Pseudophragmina (Athecocyclina) stephensoni (Vaughan). FROST and LANGENHEIM, 1974, pl.22, figs.1-9, pl.23, fig.5.

Athecocyclina stephensoni (Vaughan). ROBINSON AND WRIGHT, 1993, fig. 31.1,2,6.

Remarks: This species can be recognized by the subcircular protoconch embraced by

a much larger, distinctly reniform, deuteroconch. Radial chamber walls are incomplete or indistinct (Cole, 1964, p.C715-717). This gives the appearance of layers of concentric rings around the nucleoconch. Vaughan (1936) indicates that the test of this species is usually undulate and may be selliform (saddle-shaped). Selliform tests are common in larger foraminifera living in agitated waters.

III. BIOSTRATIGRAPHIC AND BIOGEOGRAPHIC SIGNIFICANCE

Gravell and Hanna (1938) defined the "*Discocyclina Blanpiedi–Discocylina Cookei* Zone" larger foraminiferal biozone as essentially equivalent to the Salt Mountain Limestone. The geographic extent of this zone was not clearly defined, but was recorded from the subsurface of southwestern Alabama and Jackson County, Florida. Cole (1959, 1969) indicates that these same two orbitoid foraminifera are part of his *Operculina* (= *Ranikothalia*, Robinson and Wright, 1993) *catenula* Fauna, an upper Paleocene to (?)lowermost Eocene LBF assemblage found in Haiti, Trinidad, Mexico, Venezuela, Barbados, Cuba, and the southeastern United States (Cole, 1959, 1969). Species of the *Operculina catenula* Fauna include (Cole, 1959):

Ranikothalia catenula (Cushman and Jarvis)
Actinosiphon semmesi Vaughan
Discocyclina (Discocyclina) barkeri Vaughan and Cole
Discocyclina (Discocyclina) cristensis (Vaughan)
Discocyclina (Discocyclina) weaveri Vaughan
Pseudophragmina (Athecocyclina) stephensoni (Vaughan).

Of the six regional locations of the fauna mentioned by Cole, only at the Salt Mountain Limestone is the primary zonal species, *Ranikothalia catenula*, absent. But both *Ranikothalia catenula* and *Pseudophragmina stephensoni* have been reported from the Porters Creek Formation in the subsurface of Georgia (Cole and Herrick, 1953; Cole, 1959). If this lithostratigraphic correlation is correct, it would extend the range of these foraminifera into the Danian, although Fluegeman (pers. comm.) indicates that this interval is probably Late Paleocene in age (Zone P4c). Both *Pseudophragmina (Athecocyclina) stephensoni* and *Discocyclina (Discocyclina) weaveri* are widespread across the Gulf of Mexico basin and Caribbean in rocks of Late Paleocene to Early Eocene age (Cole, 1969; Frost and Langenheim, 1974).

The genera *Discocylcina* and *Ranikothalia* were among the earliest Tertiary LBF genera, and appear to have a near worldwide distribution at their usual first appearance in the Late Paleocene. They are found in each of the major LBF faunal provinces: American, Tethyan, Indo-Pacific, and both genera were primarily open shelf dwellers (Adams, 1972; Hottinger, 1972). *Discocyclina*, however, has the widest paleolatitudinal range of any Cenozoic large foraminiferan. During the mid-late Eocene, when LBF diversity was at its highest, *Discocyclina* reached Alaska, New Zealand, and southern Australia. Evidently, either some species were tolerant of cool waters, or subtropical conditions extended into much higher latitudes (Adams *et al.*, 1990).

Using smaller benthic foraminifera,

PLATE 1

Figures

1. Equatorial view (4x) of *Pseudophragmina (Athecocyclina) stephensoni* (Vaughan, 1929) (formerly *Discocyclina cookei*), from Station 2 of Toulmin (1940b). Florida Museum of Natural History specimen UF 69497.

2. Equatorial view (4x) of *Discocyclina (Discocyclina) weaveri* Vaughan, 1929 (formerly *Discocyclina blanpiedi*), from Station 1 of Toulmin (1940b). Florida Museum of Natural History specimen UF 69496.

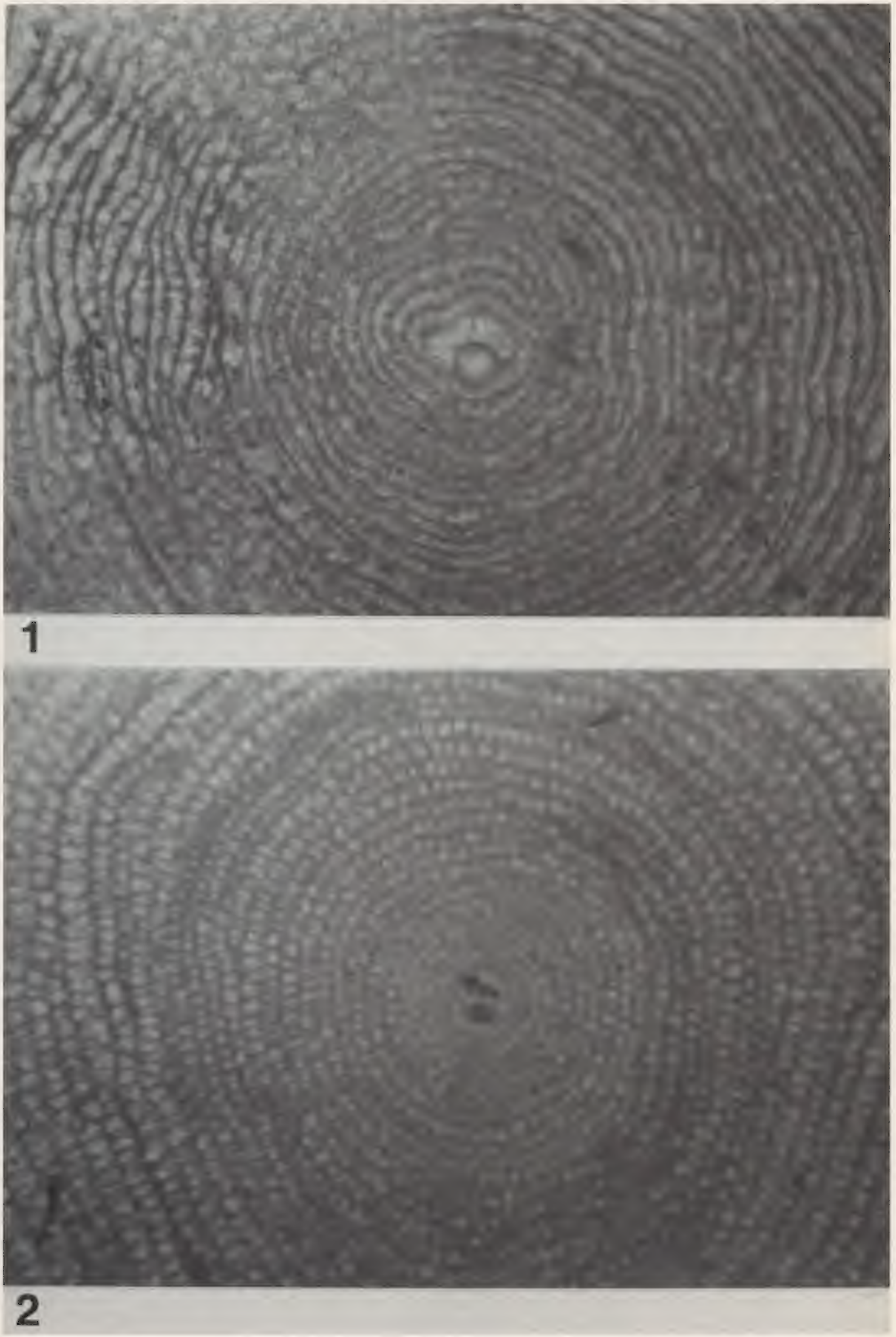

PLATE 1

Berggren and Aubert (1975) identified three circum-Atlantic/Tethyan foraminferal assemblages during the Paleocene. The first is the "Tethys Carbonate Fauna" (see Berggren, 1974), which was deposited in inner to middle neritic waters (<30-50 meters depth). The second is the "Midway-type-fauna", representing middle to outer neritic water depths (50-200 meters depth). And the third is the "Velasco-type fauna", indicating slope-rise and deeper conditions (>200 meters depth). They consider the Salt Mountain fauna to represent, "essentially, an extension of the Midway (fauna)", but the presence of discocyclinid larger foraminfera indicates strong affinities with their Tethys Carbonate Fauna.

IV. PALEOECOLOGY

Today, larger foraminifera are found almost exclusively in tropical to subtropical, oligotrophic to mesotrophic environments, such as in reefs and related facies. Nearly all harbor algal photosymbionts within their cytoplasm and their complex, compartmentalized tests are thought to be, at least in part, adapted for this purpose. Most extinct LBF are associated with similar paleoenvironments, and are inferred to have also hosted photosymbionts. When present, LBF are frequently found in great abundance and may rival corals and algae in carbonate sediment production.

According to Vaughan (1945) nearly all American discocyclinids are found in "tropical to subtropical, and south temperate latitudes," and are associated with other larger foraminifera and coralline algae. He estimates that discocyclinids ranged from "slightly below tide level to perhaps 100 meters" and probably could not tolerate temperatures below 16°C. According to Ghose (1977), large, flat discocylcinids (such as those found in the Salt Mountain) are characteristic of shallow fore-reef environments (smaller, more robust forms may be found in backreef areas near the reef core). Breard *et al.* (1994) also suggest inner neritic depths (0-30 meters) for discocylclinids of the Gulf Coast Paleocene and Eocene, as did Eva (1976) for *Pseudophragmina* in the Jamaican Middle Eocene. Fermont (1982) reports *Discocyclina* in upper to lower foreslope enviroments in the Eocene of Ein Avedat (Israel). Frost and Langenheim (1974) record *Pseudophragmina (Athecocyclina) stephensoni* in sandy, high-energy, nearshore sandy limestones of Late Paleocene age in the Chiapas, Mexico. In the Salt Mountain Limestone, the discocyclinids are primarily found in Biofacies 1, interpeted as a forereef deposit (Bryan, 1991), and according to Fluegeman (this volume), deposited in water depths of 15 to 30 meters.

PART IV
CORALS

THOMAS A. STEMANN

I. INTRODUCTION

Although the Salt Mountain Limestone has long been known as a "coral limestone," only two coral species have been formally recognized from this formation (Bryan, 1991). Vaughan (1900) described the massive corals *Stylophora ponderosa* and *?Turbinoseris alabamensis* (now considered *Actinacis alabamensis*), and noted other forms were also present but were unidentifiable due to their poor preservation. The relatively poor preservation of the Salt Mountain corals is one reason this fauna has been largely overlooked in studies of Paleogene reefs. More detailed, recent studies, however, have revealed a considerable diversity of corals (Bryan, 1991; Krumm and Santos, 1993). Recognition of the fauna as a unique Paleocene Caribbean reef community has also been hampered by earlier confusion about the age of the formation among some workers (cited in Bryan, 1991).

The Salt Mountain coral fauna is significant for two reasons. First, as the only known Paleocene coral-algal build up in the Western Hemisphere, it is an important key to our understanding of how reef communities became reestablished after the coral extinctions of the end-Cretaceous (Wells, 1956; Rosen and Turnsek, 1989; Veron, 1995). Second, at a paleolatitude of about 31-32°N (Bryan, this volume), the Salt Mountain coral community represents one of the highest latitude Tertiary age coral build-ups in the Western Hemisphere. Thus, it is also important to our understanding of latitudinal variation and geographic control of reef growth and coral communities.

The present report provides a brief description of the Salt Mountain coral fauna, its ecology and its relationship with other known Tertiary through Recent reef communities. This study is based on the collections of Jonathan Bryan and his students and by Debra Krumm. All specimens figured here will be reposited at the Florida Museum of Natural History. A complete, systematic description of the fauna will be published separately.

II. THE FAUNA

The Salt Mountain coral fauna includes 12 species, two of which were previously described from the formation by Vaughan (1900) (Table 1). Besides these 12 coral species, a single sclerite of the octocoral *?Parisis* has also been collected. Among the corals, three species are also recorded from the Paleogene of the Caribbean and Gulf Coast regions (*Madracis herricki, Cyathoseris eocenica* and *Actinacis alabamensis*). One species, *Cyathoseris ?valmondasiaca*, appears close to a species known from the European Eocene. Four species recognized here are apparently new (Table 1). Two others, *?Trochoseris* sp. and *Antillia* sp., cannot be referred to any described species and are only known from single specimens. These species are therefore left in open nomenclature. Finally, one form could only be identified to the family level, Caryophylliid sp. Table 2 presents a short diagnostic key for the Salt Mountain fauna.

Massive and explanate-laminar corals are the most diverse and volumetrically important part of the Salt Mountain scleractinian community. Corals are highly recrystallized, though considerable skeletal detail is preserved (Text-figure 1). Moldic preservation is also common, especially among platy forms. *Stylophora ponderosa* is by far the most abundant and largest (up to 1 meter in diameter) coral in the fauna. *Actinacis alabamensis* is also common and may reach 0.2 m in breadth and thickness. Locally, however, some small thickets of the thinly branched, dendroid corals, *Oculina* new sp. and *Dendrophyllia* new sp., (Text-figure 2) may be volumetrically important, especially in Biofacies 2 and 4 (Bryan, this volume). The massive, encrusting and explanate species are largely confined to the Sponge-Coral Bafflestone/Framestone Biofacies 3 of Bryan (this volume), though smaller, isolated coral heads may be found elsewhere throughout the section. To date, no robust branching forms similar to those that dominate later Tertiary reefs, such as *Acropora, Pocillopora* or branching *Stylophora* (Veron, 1986; Budd *et al.*, 1994), have been collected from the Salt Mountain Limestone.

Other than the Salt Mountain, there is only one other important Paleocene coral fauna from the Gulf Coast region (Vaughan, 1900), the corals from the Lower Paleocene Midway Group of Alabama (Table 3). Comparisons between Midway and Salt Mountain faunas are interesting because there are, in fact, no species or genera in common between the two. This is unusual because all the Midway Group species (except *Mesomorpha duncani*) belong to genera that are common in Eocene and, in some cases, younger Caribbean coral faunas (Budd *et al.*, 1992; Wells, 1956). Frost and Langenheim (1974) found *Siderastrea hexagonalis* in the Lower Eocene of Mexico, while during the Eocene *Haimesastrea conferta* and closely related congeners are a conspicuous part of Caribbean and eastern Pacific reef communities (Vaughan, 1922; Frost and Langenheim, 1974). It is highly likely that further collection from the Salt Mountain Limestone will yield some corals closely related to those found in the Midway Group.

III. PALEOECOLOGY

The massive morphology of the most common corals may suggest that the Salt Mountain Limestone was deposited at shallow to moderate water depths. Conversely, the dominance of delicately branched corals in some facies could suggest either much deeper water below effective wave base or shallow protected environments. Indeed, fossil (Alvarez *et al.*, 1991) and modern congeners of the *Dendrophyllia* sp. are often found in very deep water settings (>250 m) (Cairns, 1979; Wells, 1956). Still, the abundant crustose algae associated with and in many cases encrusting the Salt Mountain corals indicates the fauna was deposited in fairly shallow water.

A chief question concerning the fauna is whether the corals were predominately zooxanthellate (and thus similar to reefal assemblages of the later Cenozoic) or azooxanthellate. Because all the species and at least half the genera represented in the Salt Mountain collections are extinct it is difficult to precisely determine whether

TABLE 1. Corals of the Salt Mountain Limestone. Zooxanthellate and Azooxanthellate determinations based on colony morphology and systematic relationships to modern coral groups. Additional stratigraphic occurrences taken from Bryan and Huddleston (1991), Budd *et al.* (1992), Vaughan (1900) and Wells (1934).

Coral Species	**Colony Morphology**	**Zooxanthellate-Azooxanthellate?**	**Other Occurrences**
Stylophora ponderosa Vaughan, 1900	massive	Z	--
Madracis new sp.	encrusting	A/Z	--
Madracis herricki Wells, 1934	encrusting	A/Z	Mid. Eocene, Texas
?Trochoseris sp.	solitary	Z	--
Cyathoseris ?valmondasiaca (Michelin, 1843)	explanate	Z	Mid.Eoc., Paris Basin
Cyathoseris eocenica (Stemann *in* Budd *et al.*, 1992)	explanate	Z	Upper Eoc., Panama
Sideroseris new sp.	phaceloid-solitary	A	--
Actinacis alabamensis (Vaughan, 1900)	massive	Z	Eoc., Jamaica,Panama Lower Olig., Georgia
Oculina new sp.	dendroid	A/Z	--
Antillia sp.	solitary	Z	--
Caryophylliid sp.	solitary	A	--
Dendrophyllia new sp.	dendroid	A	--

or not any bore algal symbionts. In this study, colony morphology and species' systematic relationships with modern corals were used to make estimates about the presence or absence of zooxanthellae in the Salt Mountain fauna (Table 1). Using these criteria, three groups of species were recognized: zooxanthellate (Z), azooxanthellate (A) and those species (A/Z) that may have been zooxanthellate, azooxanthellate or facultatively both (*i.e.*, apozooxanthellate).

Zooxanthellate Corals

Six of the 12 Salt Mountain species were probably true zooxanthellate corals. All are most closely related to modern species that bear algal symbionts. Although *Actinacis alabamensis* belongs to an extinct family, the Actinacidae, most workers consider it to be closest systematically and ecologically to members of the reef coral family Poritidae (Bosellini and

TABLE 2. A field key to the Scleractinian corals of the Salt Mountain Limestone. Additional diagnostic information for each species is listed in parentheses. Abbreviations are cd - corallite diameter; cs - spacing of corallite centers; ns - number of septa per corallite.

I. Solitary
- A. Diameter 30-50 mm ..... *Antillia* sp.
  (trochoid; elliptical; 12 septa/cm at wall)
- B. Diameter 20-30 mm ..... *?Trochoseris* sp.
  (>30 septa/cm at wall)
- C. Diameter 10-15 mm ..... Caryophylliid sp.
  (cylindrical; ns: 40-50)

II. Colonial
- A. Branched
  - 1. Branch diameter 7-8.5 mm ..... *Sideroseris* new sp.*
    (ns:55-65; thin rods connecting septa)
  - 2. Branch diameter 3.0-4.5 mm ..... *Dendrophyllia* new sp.
    (ns: 24-48; wall porous)
  - 3. Branch diameter <3.0 mm ..... *Oculina* new sp.
    (ns:12-24; major septa w/pali; wall solid)
- B. Massive-laminar
  - 1. Corallites in series
    - a. Series parallel edge ..... *Cyathoseris eocenica*
      (platey; cd:5-12 mm; cs:2.5-10 mm)
    - b. Series radiate ..... *Cyathoseris ?valmondasiaca*
      (cup-shaped; cd:<7.5 mm; cs:1.5-5 mm)
  - 2. Corallites not in series
    - a. Solid coenosteum
      - i. Septa in cycles of 6 ..... *Stylophora ponderosa*
        (massive; cd: 1.0-0.5 mm; cs:1.0-1.3 mm)
      - ii. Septa in cycles of 10
        - aa. cd: 1.3-1.8 mm ..... *Madracis* new sp.
          (encrusting-?branched; cs: 2.0-3.0 mm)
        - bb. cd: 2.3-3.5 mm ..... *Madracis herricki*
          (encrusting-nodular; cs: 2.0-3.0 mm)
    - b. Porous coenosteum ..... *Actinacis alabamensis***
      (cd: 0.8-1.5 mm; cs: 2.0-3.0 mm)

Notes:
* *Sideroseris* new sp. may also be found as a solitary coral.
***Actinacis alabamensis* colonies are rarely preserved well enough to exhibit clear coral-CD in sectioned colonies is often significantly less than the 1.5 mm found on the holotype.

Russo, 1995). Also, *A. alabamensis* and *Stylophora ponderosa*, both grew as large, massive colonies with small (<1.5 mm) corallites, a combination of characteristics that is rare in known modern azooxanthellate corals (Coates and Jackson, 1985). Similarly, the explanate or platy corals, *Cyathoseris ?valmondasiaca* and *C. eocenica*, were almost certainly zooxanthellate because this growth form is unknown among modern Pacific or Caribbean azooxanthellate corals (Veron, 1986; Budd *et al.*, 1994). Among the solitary corals, only *Antillia* sp. is considered a near-certain zooxanthellate species because it is a member of an entirely zooxanthellate family, Mussidae, and because of its large diameter (Coates and Jackson, 1985). A single, poorly preserved specimen here attributed to *?Trochoseris* sp. may also be a zooxanthellate coral based on its possible relationship to the reef coral family Agariciidae.

Azooxanthellate Corals

Three species in the Salt Mountain probably did not bear algal symbionts (Table 1). The most common of these belongs to the genus *Dendrophyllia,* a group composed entirely of azooxanthellate corals. The solitary coral fragment assigned to the family Caryophylliidae is also almost certainly an ahermatypic coral since solitary corals belonging to this family all lack symbiotic algae. Based on its small solitary or phaceloid morphology, the specimens of *Sideroseris* sp. probably represent an azooxanthellate coral species. It is, however, a member of the important reef coral family, the Siderastreidae, and congeneric species of this extinct genus are known to co-occur with other Paleogene 'hermatypic' species (Wells, 1945; Frost and Langenheim, 1974).

A/Z Corals

Three species in the Salt Mountain fauna (M*adracis herricki, Madracis* new sp. and *Oculina* new sp.) may have been either zooxanthellate or azooxanthellate and are designated A/Z in Table 1. Given their morphology and relationship to modern species they were quite possibly apozooxanthellate corals, that is, they could survive indefinitely with or without symbiotic algae. Modern representatives of the genera *Madracis* and *Oculina* range from the Caribbean-Western Atlantic tropics north to the Mediterranean (Rezak *et al.*, 1985; Wells, 1973; Wells, 1956) and include species with or without zooxanthellae as well as apozooxanthellate species. Among modern corals, *Madracis* is the best known genus to include facultatively zooxanthellate species (Veron, 1995), but both *Madracis* and *Oculina* that are important in faunas from higher latitudes (Rezak *et al.*, 1985). Fossil occurrences from regions at the northern limit of reefal development clearly suggest that many extinct species of both of these genera were also apozooxanthellate (Allmon *et al.*, 1996; Vaughan, 1900). For instance, *Madracis herricki* of the Salt Mountain Limestone is also present in the Eocene of Bastrop County, Texas (about 30°N) where it co-occurs with a low diversity fauna of exclusively azooxanthellate corals (Wells, 1934) suggesting that it, too, is azooxanthellate or at most apozooxanthellate.

IV. COMPARISONS WITH OTHER FAUNAS

The Salt Mountain fauna is five times or more less diverse than many Neogene through Recent coral communities in the Caribbean (Budd *et al.*, 1994) and also far less species-rich than Eocene (Budd *et al.*, 1992) and Oligocene (Vaughan, 1919) reef faunas. Admittedly, the relatively small outcrop area of the Salt Mountain Limestone, its generally poor coral preservation and the comparatively few coralline facies represented all serve to decrease the number of species recorded from this formation. Still, two other important factors restricting species richness in the Salt Mountain fauna are the after effects of the end-Cretaceous extinctions (Wells, 1956; Veron, 1995) and the high latitude posi-

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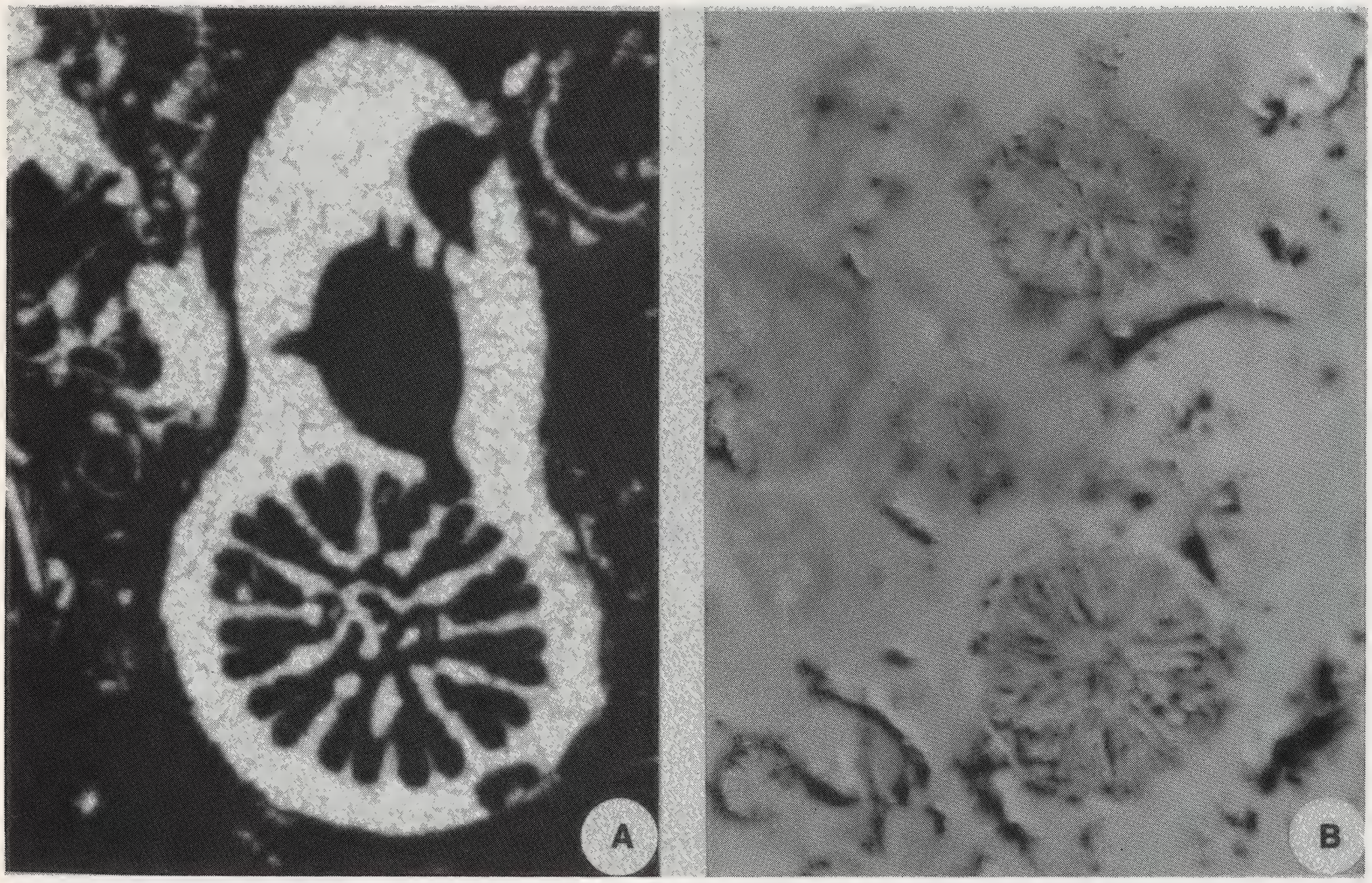
Text-figure 1. Massive and laminar corals of the Salt Mountain Limestone. A. Side view of *Actinacis alabamensis* colony, 0.8x. B. Oral view of *Stylophora ponderosa* colony, 1.25x. C. Moldic impression of *Cyathoseris eocenica* colony, 0.8x. D. Moldic impression of *Madracis* new sp., 1.0x.

A
B
C
D



Text-figure 2. Branched corals of the Salt Mountain Limestone. A. Thin-section photo of *Oculina* new sp. corallite and oblique section of branch. Note solid corallite wall and lobate ends of septa (pali), 20x. B. Polished slab photo of two *Dendrophyllia* new sp. branches. Note porous corallite walls and algal coating on larger of two branch sections, 7x.

tion of the Salt Mountain build up.

Late Cretaceous coral faunas of the Caribbean and North American region are in need of revision, but it can be said that at the generic level they are more diverse than any communities of the Gulf Coast Paleocene (Wells, 1956; Rosen and Turnsek, 1989). None of the species and only five genera of the Salt Mountain fauna, *Madracis, Trochoseris, Cyathoseris, Actinacis* and *Oculina*, can be traced back into the Cretaceous (Wells, 1956). While the K-T extinction event significantly affected scleractinians in general and zooxanthellate corals specifically (Rosen and Turnsek, 1989), this can only partially explain the low diversity in the Salt Mountain fauna.

Globally, Paleocene coral faunas are generally depauperate compared to those of the later Tertiary (Rosen and Turnsek, 1989). However, some earliest Tertiary reef coral communities may be fairly diverse. For instance, the Paleocene of northern Somalia contains 33 species and 20 genera (A. Russo cited in Rosen and Turnsek, 1989) and the Paleocene reef fauna of northcentral Pakistan includes 37 recorded species and 28 genera (Gregory, 1930). Approximately 20 genera of reef (*i.e.*, zooxanthellate-like) corals are present both in Cretaceous and in Eocene or younger Caribbean sediments but are absent in the Salt Mountain (compiled from Vaughan, 1919; Wells, 1956; Budd *et al.*, 1992). Thus, the nine coral genera recognized in the fauna (Table 1), while a higher number than in any other reported Paleocene fauna from the Western Hemisphere, actually represent less than a third of the probable standing diversity in the Caribbean and North American

region.

In terms of coral species richness, the Salt Mountain fauna is broadly similar to other Tertiary subtropical coral communities (*e.g.*, Vaughan, 1919). Among the best described of these is the Upper Oligocene Damon Mound reef of the Anahuac Formation, Texas (Frost and Schafersman, 1978). Like the Salt Mountain build-up, the Damon Mound reef also developed at relatively high paleolatitude on a local topographic high amidst a siliciclastic dominated shelf. With only about 14 species, the Damon Mound coral fauna is also a comparatively low diversity community, presumably representing a depauperate, high latitude fauna (Frost and Schafersman, 1978). Coral species richness is, therefore, comparable with that of the Salt Mountain, but, coral abundance is considerably greater in the Damon Mound reef. Also, unlike the Salt Mountain coral fauna, the Damon Mound reef community does not include a significant number of azooxanthellate or apozooxanthellate species.

The co-occurence and co-dominance of hermatypic and non-hermatypic corals in the Salt Mountain are typical of many communities at the northern limit of zooxanthellate coral growth such as in the Pliocene of Florida (Allmon *et al.*, 1996) or in the modern Gulf of Mexico or Atlantic coast of Florida (Rezak *et al.*, 1985). Among Recent reef communities, those of the Flower Garden Banks, the northernmost reefs in the Gulf of Mexico (Rezak *et al.*, 1985), are probably most similar to the Salt Mountain fauna. Like the Salt Mountain fauna, the scleractinians of the Flower Garden Banks include relatively few species, less than a third of modern Caribbean reef coral diversity. Also, the community includes several probable apozooxanthellate species of *Madracis* (Rezak *et al.*, 1985). While coral abundance in the Salt Mountain Limestone is not as high as seen in the Flower Garden Banks, the two faunas are similar in that they are both dominated by massive to laminar corals rather than rapidly growing, robust branching zooxanthellate species that dominate most later Tertiary through Recent Caribbean reefs.

V. CONCLUSIONS

The Salt Mountain coral fauna is a mixture of true reefal and non-reefal elements. It probably represents a community near the northern limit of zooxanthellate coral growth. As such, the low diversity of corals may be chiefly attributable to environmental conditions present at these high latitudes rather than the result of a delayed recovery from the K-T extinctions on tropical reefs.

Although more than 50% of the genera represented in the Salt Mountain can be traced back into the Cretaceous, the fauna does exhibit some distinctly Cenozoic aspects. For the most part, the genera that cross the K-T boundary and are pre-

TABLE 3. Vaughan's (1900) colonial scleractinians of the Midway Group, Lower Paleocene, Alabama. All are species named by Vaughan (1900). None of these species are yet known from the Salt Mountain, although congeners of all species are known from younger deposits. Only *Mesomorpha* is unknown in younger Caribbean reef coral assemblages. Zooxanthellate and azooxanthellate determinations are determined as in Table 1.

Coral	**Species Azooxanthellate**
Siderastrea hexagonalis	Z
S. (Stephanomorpha) monticuliformis	Z
Mesomorpha duncani	?Z
Oculina ?smithi	A/Z
Astrangia wilcoxensis	A/Z
Dichocoenia alabamensis	Z
Haimesiastrea conferta	A/Z

sent in the Salt Mountain Limestone (*e.g.*, *Madracis, Trochoseris*) are not significant players on Cretaceous reefs (Wells, 1956). The most dominant, massive corals in the late Paleocene of Alabama, *Stylophora, Actinacis*, and *Cyathoseris*, remain important on Eocene and Oligocene reefs worldwide (Budd *et al.*, 1992; Bosselini and Russo, 1995). Thus, the Salt Mountain fauna shows that many important Tertiary reef coral clades were already significant parts of coral communities by the late Paleocene.

Two significant absences from the Salt Mountain are corals from the families Acroporidae and Faviidae, the two most dominant scleractinian families on modern reefs (Veron, 1995; Wells, 1956). There is no clear explanation for the absence of faviids, such as the genus *Montastraea*, since these corals are generally found wherever zooxanthellate corals occur. The absence of acroporids is more understandable because their importance on the early Tertiary was not nearly so great as in the Neogene through Recent (Wells, 1956) and in the Caribbean-Western Atlantic region they apparently have always been restricted to low latitude reefs (*e.g.*, Frost and Schafersman, 1978; Logan, 1988; Rezak *et al.*, 1985).

Finally, it should be stated that at a paleolatitude of 30-31º N, the Salt Mountain fauna is a "high latitude" community only in relation to the Gulf of Mexico and Caribbean region. There is probably more luxuriant reef coral growth today on the Bermuda Platform at >32° N than anywhere in the northern Gulf of Mexico since at least the Cretaceous (Logan, 1988). Similarly, modern Japanese coral faunas at >30°N are orders of magnitude more species rich than any northern Gulf communities (Veron, 1992). In the European Tethys region, significant coral reef growth occurred at >40°N until the Late Miocene (Wells, 1956). Thus on a global scale, reef coral growth in the Gulf of Mexico-Western Atlantic region is unusually restricted. The existence of a low diversity, marginal reef fauna in the Salt Mountain Limestone suggests that this restriction of reef growth in the Gulf of Mexico and the environmental conditions contributing to it have been in place for at least 55 million years.

PART V
SALT MOUNTAIN PATCH REEF SURVEY

DEBRA K. KRUMM

I. INTRODUCTION

A survey of a coral-algal-sponge patch reef from Bryan's (1991) Biofacies 3 was conducted using a three-square-meter by two-square-meter grid system. The objective was to map a portion of the Paleocene reef to determine whether the exposure was a true framework or a non-structured buildup and to identify the corals and associated bioeroding bivalves. Paleocene frameworks are rare, particularly those containing hermatypic corals (Fagerstrom, 1987; Bryan, 1991). The relationship between borers and host corals dates back to the appearance of scleractinian corals in the Triassic (Kleemann, 1990). Endolithic bivalves tend to emerge relatively unscathed from mass extinction events, while their hosts can suffer significant losses (Kauffman, 1988; Kleemann, 1990). The presence in the Salt Mountain Limestone of Paleocene coral patch reefs offers the opportunity to look at scleractinian and endolithic bivalve diversity at a point during the recovery stage following the end-Cretaceous worldwide mass extinction event.

II. METHODS OF STUDY

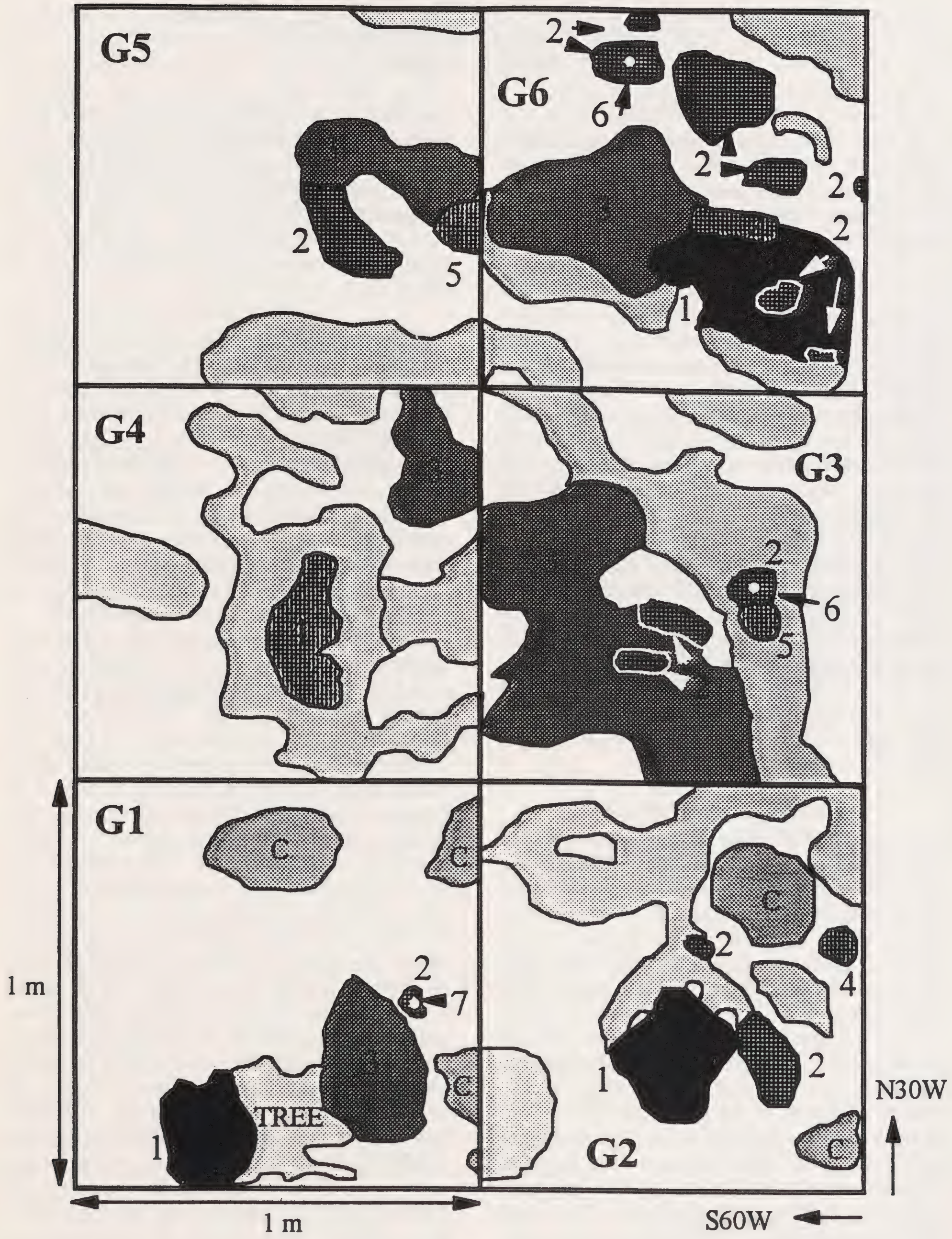
A series of six one-meter-square grids were mapped on an exposed portion of the Salt Mountain Limestone containing Bryan's (1991) Biofacies 3. The site for the grids is located in the upper occurrence of Biofacies 3 (see Bryan, 1991, this volume, and Fluegeman, this volume) and was based on amount of exposure. Text-figure 1A illustrates the layout of the grids, while Text-figure 2 is a photograph of the site. The set of six grids trends N30W and S60W as measured from the southeastern corner of Grid 2 (Text-figure 1A). The grids were laid out on a slope of approximately 20° following the exposed surface, not the bedding plane. The beds dip approximately 7° to the south (see Bryan, 1991, p. 428). The corals exposed on the hillside within the grids were mapped to scale. The locations of mollusks were noted on the maps. No other macrofossils were observed. Microfossils were not examined in this study. After mapping and photographing, samples were taken of the corals, mollusks, and matrix. The corals were cut and polished in the lab and thin sections were made of the matrix. The corals were identified by Ann F. Budd and Thomas A. Stemann (see Stemann, this volume) of the University of Iowa.

III. RESULTS

Lithologies. The matrix is micritic and contains bioclasts of foraminifera, sponges, and algae. It surrounds some of the corals. Other corals form part of a boundstone that is cemented together with sponges and algae. The thin sections reveal a fine-grained muddy matrix with branching corals, foraminifera, bryozoa, and with very little calcareous algae. Fluegeman (this volume) places Biofacies 3 into the benthic foraminiferal *Discocyclina-Pseudophragmina* assemblage.

Corals. The results of the patch reef survey are presented in Text-figures 1A and 1B. Coral diversity is low. Only five species were identified. This can be compared to 65 coral species reported from the Oligocene Chiapas Formation of Mexico by Frost and Langenheim (1974) and 175 species reported from the Miocene to the Recent for the Caribbean region by Budd, Stemann, and Johnson (1994). Of the five species, four are hermatypic while *Dendrophyllia* is ahermatypic. *Actinacis alabamensis* and *Stylophora ponderosa* were described by Vaughan (1900) and reported from the Salt Mountain Limestone by Toulmin (1940) and Bryan (1991). The other three species, *Haimesastraea conferta* Vaughan 1900, *Dendrophyllia* sp., and *Cyathoseris* sp., have not previously been reported from the Salt Mountain Limestone. *Dendrophyllia* exhibits a branching dendroid morphology, while the other species, *H. conferta, A. alabamensis, S. ponderosa,* and *Cyathoseris* exhibit more ramose to massive morphologies.

Endolithic Bivalves. Bryan (1991) reports specimens of the chemically-boring bivalve genus *Lithophaga* boring into a laminated algal boundstone from Biofacies 1. The specimens are confidently assigned



Text-figure 1A. Field map of an exposed section of a Salt Mountain Limestone patch reef from Bryan's (1991) Biofacies 3. Grid maps how the relationships of the corals, associated molluscs, and matrix (G=GRID). Each grid map is a square meter. Text-figure 1B contains the keys to numbers, letters, and symbols.

FAUNAL LIST FOR SALT MOUNTAIN GRIDS 1-6

NUMERICAL KEY:

Scleractinia:

1. *Actinacis alabamensis* Vaughan, 1900
2. *Dendrophyllia* sp.
3. *Stylophora ponderosa* Vaughan, 1900
4. *Haimesastraea conferta* Vaughan, 1900
5. *Cyathoseris* sp.

Mollusca:

6. Gastropod
7. *Lithophaga* aff. *nigra*

SYMBOL KEY:

- *Actinacis alabamensis*
- *Dendrophyllia* sp.
- *Stylophora ponderosa*
- *Haimesastraea conferta*
- *Cyathoseris* sp.

C - Unidentified coral

- Matrix
- Cover

Text-figure 1B. Faunal list for Grids 1-6 of the Salt Mountain patch reef represented in Text-figure 1A. Keys to numbers, symbols, and letters from the grid maps.

to the genus based on shell morphology. Also, the borehole cuts across the layers of algae rather than conforming to them or causing the layers to grow around the bivalve as would be the case for a nestler or a burrower. The borehole was not lined. Bryan (1991) also illustrates a boring from Biofacies 2 that bears a strong resemblance to *Gastrochaena (Rocellaria) ovata* Sowerby, 1834. The outline of the shell is consistent with gastrochaenids, as is the thick lining around the siphons and thinner lining around the bivalve (Carter, 1978). The specimen is very small, however, so identification to species level is tentative.

Only one specimen of *Lithophaga* was found in the grids mapped for this project. It was associated with *Dendrophyllia* sp. in Grid 1 (see Text-figure 1A), although Bryan (1991) mentions other bivalve borers from Biofacies 3. Because of the

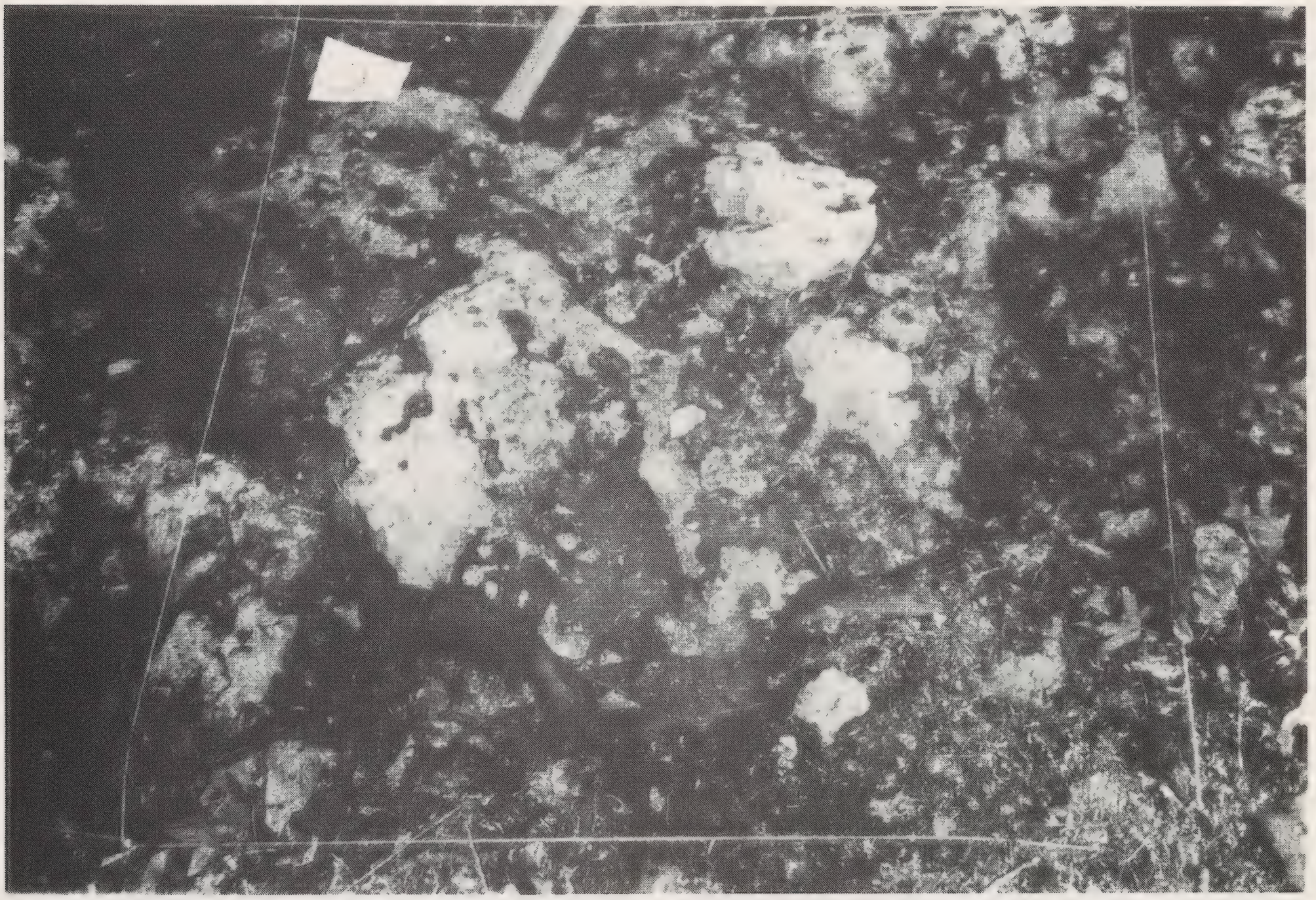
Text-figure 2A. Field position of Grids 1-6 laid out on exposed patch reef (Text-figure 1A). Grid 1 is in the lower right corner. Grids 5 and 6 are in the upper left corner of the photo. Each grid is a square meter in size. The hammer between Grids 2 and 3 is for scale.

nature of the preservation, it was not possible to determine whether the bivalve was boring into branches of *Dendrophyllia* or into associated encrusting or laminated substrata or both. The shell morphology clearly resembles *Lithophaga*. No borehole linings were visible. The specimen bears a strong resemblance to Bryan's (1991) specimen from Biofacies 3. The outlines of the shells and the lack of linings place the specimens in the subgenus *Lithophaga* with similarities to *L. (L.) nigra*, but are small for the species (Abbott, 1974; Dudley, 1986).

IV. SUMMARY AND CONCLUSIONS

The coral-algal-sponge boundstone of Bryan's (1991) Biofacies 3 represents a series of patch reefs in the sense of Fagerstrom (1987). The frameworks are cemented together to form independent topographically raised structures. However, the high diversity normally associated with scleractinian reefs is absent.

Several factors may have affected coral diversity. Bryan (1991) points out that the Salt Mountain reefs may have been growing at the northern limits of the coral species' temperature ranges. Another major factor may have been the slow recovery rate of coral species after the mass extinction of the end of the Cretaceous. Water depth was apparently not a factor. Fluegeman (this volume) places the water depth over the patch reefs at less than five meters based on the presence of the *Discocyclina-Pseudophragmina* assemblage. He describes Biofacies 3 as representing the stabilization of reef



Text-figure 2B. Close-up of Grid 2 illustrating exposures of coral and matrix, along with portions covered by vegetation.

development in the Salt Mountain Limestone. Although few endolithic bivalves were found, those present in the patch reef exhibit typical morphologies and modes of life similar to modern western Atlantic species. The Salt Mountain represents an initial, post-Cretaceous re-establishment of scleractinian corals (with their endolithic bioeroders) as reef framework constructors.

PART VI
ECHINOIDS

BURCHARD D. CARTER

I. CHARACTERISTICS OF THE SALT MOUNTAIN ECHINOID FAUNA

Echinoids, it seems, were volumetrically a major part of the living fauna of at least some facies of the Salt Mountain Limestone. Smith and Johnson (1887, p. 20) commented on the "...great numbers of the spines and plates of echinoderms..." in the lower beds of the sole outcrop, and again (p. 21) that ..."the only recognizable fossils are the spines and plates of echinoderms and great masses of corals". Langdon (1891, p. 599) spoke of the "...characters of the Salt Mountain Limestone - i.e. corals and spines of echinoids...". Vaughan (1900, p. 31) also mentioned echinoid spines as an obvious component in the lower 6 meters (20 feet) of his measured section. Bryan (1991, p. 428-430) indicated the presence, and even prevalence, of echinoderm fragments in three of his four biofacies.

This obvious numerical abundance, however, belies a remarkably low apparent diversity. Toulmin (1940, p. 109) reported five recognizable echinoderm taxa from the Salt Mountain. Of these, one is a crinoid (*Rhizocrinus cylindricus*? Weller) and one is a seastar (*?Goniaster mammilata* Gabb). The other three are regular echinoids, which he assigned to *Dorocidaris, Salenia,* and *Loriolia*. Toulmin also recorded additional fragmentary material, including "...three or four kinds of spines..." suggesting that additional, unrecognizable echinoid taxa might have been present.

Cooke (1959) also records low echinoid diversity from the Salt Mountain Limestone, reporting only two or three genera of regular echinoids. Two of these, certainly from the Salt Mountain, are cidaroids, assigned by Cooke to *Cidaris* sp. aff. *splendens* (Morton, 1841), and *Tylocidaris salina* Cooke, 1959. The third, also a regular echinoid, is *Gagaria salis* (Cooke, 1941). This latter is based upon a single "badly corroded" specimen from the locality of Salt Mountain, but uncertain stratigraphic position. It may have come from the Oligocene Marianna Limestone.

Table I records the known echinoid species from the Salt Mountain Limestone. It is constructed so as to be as inclusive of reported occurrences as possible, though critical of prior taxonomic assignment. The systematic paleontology upon which the table is based is presented in a separate section of the paper.

The age of the Salt Mountain Limestone falls within the earlier part of the Late Paleocene (Bryan, this volume). Correlative units in the Gulf Coastal Plain have no reported echinoid fauna, though I have collected *Linthia* sp. cf. *alabamensis* from the base of the Nanafalia Formation in southeastern Alabama. However, the Vincentown Sand of New Jersey, which is probably partially correlative with the Salt Mountain, has a rich echinoid fauna. Cooke (1959) reports 10 species from the Vincentown, including the following relevant species: *Cidaris splendens, Tylocidaris walcotti, Salenia tumidula,* and *Echinopsis diatreta*. Each of these has, or may have, a congeneric counterpart in the Salt Mountain.

II. ECOLOGICAL IMPLICATIONS OF THE FAUNA

The most striking aspect of the known echinoid fauna of the Salt Mountain Limestone is the lack of irregular echinoids. Even among the reported debris – pedicillariae, spines, test fragments, and lantern fragments according to Toulmin (1940, p. 109) – the probability is that it derives from regular echinoids. First, fragments of irregular tests would be immediately recognizable. Second, irregular echinoids typically do not have large, robust spines which would be an obvious component of rocks. Third, excepting the Orders Clypeasteroida (whose only Paleocene representative is a rare African species) and the Oligopygoida (whose record begins in the Eocene) most irregular echinoids lack lanterns in the adult stage. Only the relatively uncommon Holectypoida might be expected to have contributed irregular lanterns to a Paleocene deposit in North America. (However, it should be noted that holectypoids, for example *Echinoneus*, do inhabit Recent reef environments.) Finally, any environment with little enough water agi-

TABLE I. Echinoid species known from the Salt Mountain Limestone.

Taxon recognized herein	Previously named	Source
"*Cidaris*" sp.	*Dorocidaris; Cidaris* sp. cf. *splendens*	Toulmin, 1940; Cooke, 1959
cidaroid indet.	*Tylocidaris salina*	Cooke, 1959
Stereocidaris? sp.	none	J. Bryan, pers. comm.
Salenia? sp.	*Salenia*	Toulmin, 1940
Gagaria? salis	*Gagaria salis*	Cooke, 1959
Echinopsis? sp.	*Loriolia*	Toulmin, 1940

tation to preserve complete tests, or even fairly complete, recognizable regular echinoid fragments, should also allow preservation of irregular species, were they present (Kier, 1977a).

The most obvious explanation for the lack of irregular echinoids in the Salt Mountain Limestone is that the mixed cobbly/muddy substratum provided an unburrowable habitat for a mobile deposit feeder. Echinoid species which burrow in muddy bottoms often have test structures that are highly adapted to maintaining a steady supply of fresh seawater through a dorsal tunnel, and funnelling waste water into a posterior one. Echinoids that inhabit coarser bottoms are not faced with similar hydrologic problems and lack these highly specialized adaptations (Smith, 1984; Carter *et al.*, 1989). Thus, though one irregular echinoid species might be able to burrow into muddy sediment, or another into gravel, the mixture of the two textures might exclude either species.

Alternately, the ability to burrow into gravel-rich sediments simply might not have existed in the Paleocene, either because taxa so adapted had not yet evolved, or because the niche had not yet been refilled after the Late Cretaceous extinction. As discussed below, far too little is known about the echinoid faunas of Mesozoic reefs (and early Cenozoic ones as well, for that matter) to decide if this is a problem of "recovery" or of the appropriate traits not having evolved at all by the early Cenozoic.

Modern reefs do have a small complement of burrowing irregular echinoid species. Kier and Grant (1965) report a fauna from rock bottoms on and near Recent reefs in the Florida Keys including the regular echinoids *Eucidaris tribuloides, Diadema antillarum, Arbacia punctulata, Echinometra lucunter, Echinometra viridis*, and the irregular echinoids *Echinoneus cyclostomus* and *Brissus unicolor*. I have seen or collected several of the same species, including both the irregulars, from the shore adjacent to a rocky bottom with scattered patch reefs off the coast of Kingston, Jamaica. Prager and Ginsburg (1989) demonstrated that the spatangoid *Meoma ventricosa* burrows among large rhodoliths on the fore-reef slope of southern Florida.

Dollfus and Roman (1981) give the life habits of numerous species of Red Sea echinoids. The following summary of that work is augmented by Nebelsick (1992). Reef and rock dwelling regular echinoids include *Eucidaris metularia, Phyllacanthus imperialis, Diadema setosum, Temnopleurus toreumaticus, Microcyphus rousseaui, Nudechinus scotiopremnus, Tripneustes gratilla, Parasalenia poehli, Echinostrephus molaris, Echinometra mathaei, Heterocentrotus mamillatus, H. trigonaris, Echinothrix calamaris* and the echinothuriid *Asthenosoma varium*. These 14 species explicitly cited as reef-dwellers by Dollfus and Roman represent approximately 54% of the regular echinoids (total of 26 species) they recorded. The authors did not provide any ecological information for several of the remaining species, so the proportion may be higher

or lower than 54%. Reef-dwelling irregular echinoids in the region include only two species of a total of 28 (7%). *Clypeaster reticulatus* apparently lives epifaunally and *Brissus latecarinatus* infaunally. Seven additional irregular species were not attributed to any environment, but all can be inferred not to have inhabited gravel bottoms based on their test forms.

The association of irregular echinoids, often species of the Recent reef-dwelling genera, with reef and reef-like deposits are known back through the Neogene and into the Oligocene. The algal buildups of the Lower Oligocene Bridgeboro and Florala Limestones of the eastern Gulf Coast (Manker and Carter, 1987; Bryan, 1993) have a fauna including not only cidaroids and other regular echinoids, but also irregular echinoids of the genera *Clypeaster* (probably epifaunal), *Brissus* (probably infaunal), *Macropneustes* (an infaunal species similar in morphology to Recent *Meoma ventricosa*), and possibly *Plagiobrissus*(?). Donovan and Veale (1996) document the persistence of the *Echinoneus - Brissus* association with reef-related facies in the Caribbean from the Late Oligocene to the present. I am not familiar with any studies of Eocene framework reefs in the Western Hemisphere that include information on the echinoid faunas, but a small Upper Eocene probable patch reef at Gebel Mokattam, near Cairo, Egypt, interestingly has eight or nine echinoid species in its calcarenitic flanking beds, of which seven (including species of *Sismondia, Fibularia, Agassizia, Schizaster, Eupatagus,* and *Echinolampas*) are irregulars (Roman and Strougo, 1988; Carter and Hamza, 1994). The genus *Brissus*, including species very similar in form to, if not identical with, *B. unicolor*, is known from the Eocene of the Caribbean (Kier, 1984; Donovan and Veale, 1996). *Echinoneus* apparently ranges back only to the Oligocene. Thus, if the Salt Mountain Limestone is typical of Paleocene reefs, their echinoid faunas were completely dominated by regular echinoids, and irregular echinoids may have begun moving into reef habitats, or back into reef habitats, only in the Eocene, being certainly well established there by the Oligocene.

Pre-Paleocene reef echinoids are even less well documented. Prior to the mid-Jurassic there were no irregular echinoids at all, but all the orders of irregulars had appeared by the end of the Jurassic, excepting the Clypeasteroida (Kier, 1977b; Smith, 1989). The Late Jurassic (Oxfordian) of Europe includes extensive reef deposits. The reefal facies were all originally included in the Rauracian local stage (Wilson, 1975). In their tabulation of echinoid species described through 1924, Lambert and Thiery (1909-1925) list about 130 nominal species of echinoids specifically from the Rauracian. Of these, about 29 (22%) are irregulars: all holectypoids and cassiduloids. (At the generic level the percentage of irregulars is 34%, a fact to keep in mind in light of Mr. Lambert's tendency to create and accept thoroughly oversplit taxa). Interestingly, the list includes the earliest members of the Suborder Echinoneina, whose Recent relatives are common reef-dwelling irregulars.

Of course, not all Rauracian rocks were reef framework facies, and so it is not possible to know how many of these irregular echinoids lived on a reef proper. Smith (1984) records 19 echinoid species from various subfacies of "rubbly algal gravels" and "patchy development of corals, interpreted as a lagoonal patch reef ..." in the English Jurassic. Of these, only two (~10%) are irregular echinoids; both are cassiduloids. One of these is very rare, and is known only from fragments in an oosparite associated with the reef. The other is fairly common, even as whole tests, in this same facies and in another oolitic sand, but is also known from a relatively small number of whole tests and fragments in the reefal facies, particularly the algal rubble. Whether the species actually inhabited the reef rubble or not is debatable, but its more common occurrence in the oolitic flanking beds argues against it.

Cretaceous reefs are widely distributed in North America, particularly in the subsurface (*e.g.*, the Stuart City trend of the Edwards Limestone of Texas, and the equivalent "Golden Lane" Mexican Cretaceous reefs). Surface exposures of Cretaceous reefs do exist, for example the Edwards includes patch reefs in surface

exposure, but I have not located any specific studies which allow relating echinoid species to any particular lithofacies. Cooke (1946; 1955) lists a number of species from the Edwards Limestone and equivalents (the Fredricksburg Group) of the southern mid-continent region. He identifies only one species (the saleniid regular *Goniopygus zitteli*) from the Edwards itself, but lists an additional four species from unspecified Fredricksburg Group strata. Of these, three are regulars and the fourth (the spatangoid *Heteraster texanus*) is irregular. Test morphology of the latter, and its common occurrence in the fine grained facies of the Goodland Limestone, suggests a preference for burrowing into consistently fine substrata, so it probably does not occur in the reef facies of the Edwards. Obviously, the Edwards has an overall depauperate echinoid fauna in outcrop, and no data are available to tell how many of the few echinoid species occur in the reefal sediments. In whichever facies they do occur, it is obvious that the fauna is dominated by regular echinoids. It remains a source of frustration that characterization of reefal echinoid faunas is so difficult in one of the most reef-rich time intervals, particularly the one immediately preceding a major mass extinction.

III. SYSTEMATIC PALEONTOLOGY

Class ECHINOIDEA Leske, 1778
Subclass PERISCHOECHINOIDEA M'Coy, 1849
Order CIDAROIDA Claus, 1880
?Family CIDARIDAE Gray, 1825
?Subfamily CIDARINAE Gray, 1825
?Genus CIDARIS Leske, 1778

"CIDARIS" sp.
Plate 1, figures 1a,b,c,2

Dorocidaris TOULMIN, 1940, p. 109.
Cidaris splendens (Morton) (part). COOKE, 1941, p. 5, pl. 1, fig. 12.
Cidaris sp. aff. *C. splendens* (Morton). COOKE, 1959, p. 10, pl. 1, fig. 11.

MATERIAL: Three test fragments from Toulmin's collections in the FMNH (UF 69500); unspecified number of fragments, including a figured specimen, from Cooke, 1959 (USNM 498879a); one complete test (the first known complete test of the species) collected by Stephanie Schroeder, now in the FMNH (UF 77000), one complete test, collected by Jonathan Bryan and probably of this species, at the Geological Survey of Alabama. I have not seen this last specimen.

REMARKS: Toulmin (1940) listed three generic names of echinoids from the Salt Mountain. In the material from his collections at the FMNH are three lots of specimens each labelled with one of these names, and it is likely that these are the basis for his generic list. One of the lots (UF 69500) is labelled "*Dorocidaris* sp. cf. *D. splendens*. Cidaroid genera are, unfortunately, based upon characteristics that are very unlikely to be preserved in fossil material, and *Dorocidaris* is now considered a synonym of *Cidaris*, a genus for which "...no valid fossil species has yet been described..." (Fell, 1966). Thus, Toulmin's assignment cannot be retained. I have not seen Cooke's material in the USNM, but his figured specimen is decidedly similar to Toulmin's material.

DESCRIPTION: There are three test fragments in Toulmin's lot (UF 69500), each very small, and each containing both partial ambulacra and interambulacra. The largest fragment (figured in Plate 1, figure 2) measures 2.9 mm wide, and includes a full interambulacrum and both adjacent half interambulacra. It is also only 2.7 mm high and reaches nearly, if not completely, from the peristome to the periproct. Thus, it is from an exceptionally small individual, roughly 5 mm total diameter as a gross estimate. The other two fragments are less complete, and probably come from slightly larger individuals, but still on the order of 10 mm total diameter or less. The ambulacra include nonconjugate (separated, in fact, by a distinct ridge) pore pairs, distinctly inclined to the axis of the ambulacral column. Each interambulacral plate bears a single, proportionally large, perforate, noncrenulate tubercle, surrounded by a single circle of coarse scrobicular tubercles. On the smaller two individuals, this scrobicular ring is in immediate contact with that of the adjacent plate, but on the largest, the

plate corners bear additional coarse tubercles beyond the scrobicular ring. These are almost, but not quite, as large as the scrobicular tubercles. Toulmin's specific assignment is consistent with one made (apparently) independently by Cooke for different material (see below). Based upon the material available to Toulmin it is only possible to conclude that they come from a cidaroid, and probably a cidarid, echinoid. Standard practice is now to label such taxa "*Cidaris*" sp. As discussed below, the assignment of this species to *"Cidaris" splendens* is probably incorrect, so it is herein treated as "*Cidaris*" sp.

Cooke (1941, 1959) records a cidaroid from the Salt Mountain that he states is similar to *Cidaris splendens* of the Vincentown Sand of New Jersey, only smaller. His single fragment is about 15 mm wide by 15 mm high, and includes much of an entire interambulacral column with both adjacent half-ambulacra. It is decidedly similar to the fragments in Toulmin's collection, and I do not doubt they are conspecific. The only difference is that there are more granular secondaries in the material figured by Cooke, but this is probably because it comes from a larger specimen, with more area on the extrascrobicular part of the plate. The structure of Cooke's fragment is, as was Toulmin's, consistent with a member of the Cidaridae, but since genera are virtually impossible to distinguish without pedicellariae, current practice would be to call the species "*Cidaris*" sp. cf. *splendens*. Incidentally, Cooke suggests that because this specimen is so much smaller than those from the Vincentown Sand, it probably represents a distinct, unnamed species. Size notwithstanding, the tuberculation of the two is distinct enough that he is probably right about this, so his material is herein distinguished from *C. splendens* (Morton), and joins Toulmin's specimens in "*Cidaris*" sp. in this report.

The specimen found by Stephanie Schroeder (figured in Plate 1, figures 1a,b,c) and the one found by Bryan are essentially identical to the material of Toulmin and Cooke. These are the only complete tests of the species known.

?Subfamily STEREOCIDARINAE Lambert, 1900
?Genus STEREOCIDARIS Pomel, 1883

STEREOCIDARIS? sp.
Plate 1, figure 3

MATERIAL: Three matrix encrusted fragments which each include part of a single interambulacrum and one adjacent half ambulacrum, found loose on the Salt Mountain Limestone outcrop by Bryan. Two of the three specimens (UF 76998) are very poorly preserved, and include fewer plates, but are clearly identical with the third (UF 76999), upon which the following description is based.

PLATE 1

Figures
1a-1c. "*Cidaris*" sp. UF 77000.
1a. Lateral view, x2.
1b. Apical view, x1.5. Standard orientation is not certain, but the specimen may be oriented with ambulacrum I toward top of page.
1c. Oral view, x1.5. If ambulacra are properly identified, specimen is in standard orientation.
2. "*Cidaris*" sp. UF 69500. Interambulacral fragment with adjacent half-ambulacra, x12.
3. *Stereocidaris?* sp. UF 76999. Interambulacral fragment with one attached half-ambulacrum, x1.
4. *Salenia?* sp. UF 69498.
4a-c.Isolated ambulacral fragments, x10.
5. *Echinopsis?* sp. UF 69499.
5a-b. Isolated ambulacral fragments, x10.
5c. Isolated interambulacral fragment, x10.
5d. Enlargement of 5b, x20.
(All specimens are darkened with red dye and lightly coated with ammonium chloride.)

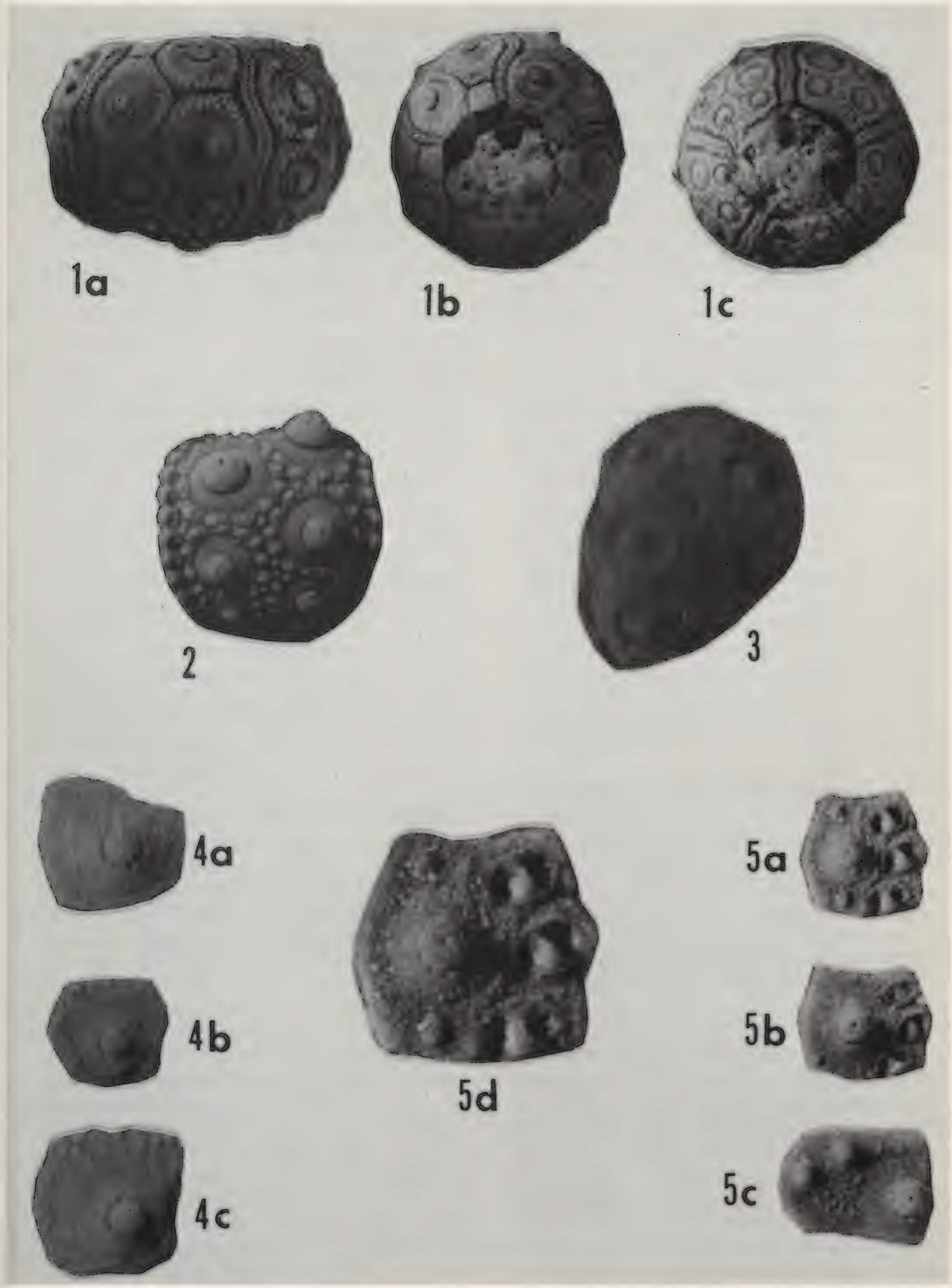


PLATE 1

DESCRIPTION: The exposed portion of the best test measures about 30 mm in height and width. There is some etching and/or abrasion of the surface, but surface detail is visible in some places. The primary interambulacral tubercles are perforate and subcrenulate, and the scrobicular tubercles surrounding the depressed scrobicle are small and sparse. In the extrascobicular areas, the secondary tubercles are aligned in distinct rows, on pronounced ridges, radiating away from the primary. The most apical preserved primary tubercles are still at least a plate distance away from the apical system. They are somewhat reduced, but none is entirely atrophied. The ambulacral pores lie in a distinct, slightly sinuous groove, and are nonconjugate. Though an exact generic, or even subfamilial, assignment is not possible, the subcrenulate tubercles and nonconjugate pores suggest the Family Cidaridae, and either the stereocidarine or cidarine subfamily. The somewhat sinuous ambulacra tend to favor the former, so I herein refer to this species as *Stereocidaris?* sp., even though it is not certain that any of the adapical primary tubercles are atrophied.

Family and Subfamily INCERTAE SEDIS

INDETERMINATE CIDAROID

Cidaris splendens (Morton) (part). COOKE, 1941, p. 5, pl. 1, figs. 13-15.
Tylocidaris? salina COOKE, 1959, p. 12, pl. 1, figs. 12-14.

MATERIAL: Three detached spines, figured in Cooke, 1959 (USNM 498879b).

DESCRIPTION: Cooke (1959) based *Tylocidaris salina* upon slightly fusiform spines and no test material. The generic assignment was probably predicated upon the fusiform shape of the spines, Cooke is not explicit on this point. However, though spine morphology can be characteristic of *Tylocidaris*, the diagnostic spines are typically much more clavate than fusiform in the genus. (Compare the *T. macneili* spine in Cooke's plate 1, fig. 4, with his figures of *T. salina*). Small, slightly fusiform spines such as the latter are not diagnostic, and the generic assignment, though reasonable, is far from certain. I refer to these spines as "indeterminate cidaroid" herein.

Subclass EUECHINOIDEA Bronn, 1860
Superorder ECHINACEA Claus, 1876
Order SALENOIDA Delage and Hérouard, 1903
Family SALENIIDAE L. Agassiz, 1838
Subfamily INCERTAE SEDIS

SALENIA? sp.
Plate 1, figures 4a,b,c

Salenia TOULMIN, 1940, p. 109.

MATERIAL: Toulmin's material identified as *Salenia* sp. (UF 69498), comprises three very small test fragments, each of which is a single interambulacral plate.

REMARKS: Because no ambulacral, apical, or peristomal characters are known, generic assignment must be uncertain. The tubercle morphology is certainly consistent with the genus *Salenia*, and the genus is a fairly common, easily recognized, often reef-dwelling regular echinoid. Toulmin's generic identification is quite likely correct, but in order to emphasize the uncertainty, I herein refer to his species as *Salenia?* sp.

DESCRIPTION: Interambulacral plates small, the largest measuring about 1.9 mm in height and 2.2 mm in width. The tubercles are very large, prominent, imperforate and crenulate. Their diameter is impossible to relate to the total plate size, because they blend smoothly into the scrobicle, which is not at all depressed. The tubercle and scrobicle together, however, take up nearly 70% of the plate height. There are two or three rows of secondary tubercles restricted to one edge of the plate, probably the adoral, flexing slightly onto the interradial suture.

Order TEMNOPLEUROIDA Mortensen, 1942
Family GLYPHOCYPHIDAE Duncan, 1889

ECHINOPSIS? sp.
Plate 1, figures 5a,b,c,d

Loriolia TOULMIN, 1940, p. 109.

MATERIAL: Toumin's lot at the FMNH (UF69499) includes three test fragments, two of which are single ambulacral plates and the third a single interambulacral plate.

REMARKS: The genus *Loriolia* is restricted to the Lower Cretaceous, and belongs to an order (Hemicidaroida) restricted to the Mesozoic, so Toulmin's generic assignment of this specimen is highly unlikely.

DESCRIPTION: The ambulacral plates (figured in Plate 1, figures 5a,b,d) are trigeminate, apparently with simple diadematoid compounding. The pores are quite large, and the pores within one pair are separated by a high ridge. The large, prominent tubercles are crenulate and perforate. On one of the plates, the primary tubercle is flanked by a pair of smaller secondaries (Plate 1, figures 5a,d). The one on the adapical side of the plate is nearer the perradial suture than the one on the abapical. On the other ambulacral fragment (Plate 1, figure 5b) the secondaries are apparently not preserved, but a distinct bump on the corner at the perradial suture and the abapical edge, if it is the remains of a tubercle, indicates that the position of the secondaries is not consistent from plate to plate. No scrobicular tubercles are preserved on either fragment. The interambulacral plate (Plate 1, figure 5c) is distinctly wider than high, and has three large perforate, crenulate tubercles. One lies near the adradial suture, closer to the adapical(?) suture than the abapical, and is slightly larger than the other two. These lie at the opposite end of the plate, with the more adapical(?) of the two a little closer to the interradial suture than the other. They are approximately equal in size. Assignment of this material to a genus is essentially impossible. The ambulacral compounding and tubercle morphology place them in either the Order Hemicidaroida (where Toulmin put them) or the Family Glyphocyphidae of the Order Temnopleuroida. There are not any obvious sutural pits on the plate edges, as would be expected of most glyphocyphids, but the fragmentary nature of the specimen would make indistinct sutural sculpture easy to miss. It is interesting to note, in this light, that the glyphocyphid genus *Echinopsis*, which has virtually no test sculpturing, is reported from the age-equivalent Vincentown Sand by Cooke (1959), who assigns *Cidaris diatretum* Morton to the genus. This species is known only from the holotype, which unfortunately is lost. Comparison, then, must be with the drawings of Clark (1915). In these drawings the ambulacral structure of *E. diatreta* are very much like that of the Salt Mountain species, but the interambulacral structure is clearly different. This indicates that the two are not conspecific. The type species of *Echinopsis* (*E. elegans* Agassiz from the Eocene of France) has proportionally much smaller tubercles than either of these species, and assignment of the American material to that genus should be considered tentative. Thus, I herein treat Toulmin's species as *Echinopsis?* sp.

Family INCERTAE SEDIS

GAGARIA? SALIS (Cooke)

Thylechinus (Gagaria) salis COOKE, 1941, p. 13, pl 2, figs. 12-14.

Gagaria salis (Cooke). COOKE, 1959, p. 17, pl. 3, figs 7-9.

MATERIAL: Cooke's third Salt Mountain species, *Gagaria salis* (Cooke, 1941) is based upon a single "badly corroded" specimen (USNM 166497).

REMARKS: The holotype of the species comes from the locality of Salt Mountain, but uncertain stratigraphic position. Thus, the suspicion must be entertained that the specimen is actually from the Oligocene Marianna Limestone, which outcrops just to the north of the Salt Mountain Limestone. Cooke suggests that the tuberculation and peristome serve to distinguish this species from the common Oligocene *G. mossomi*, but the poor nature of the specimen does not rule out the possibility of the specimen belonging to the Oligocene species. Assuming that the specimen did actually come from the Salt Mountain, it is interesting that *Gagaria* is otherwise unknown from the Paleocene anywhere in the world, and unknown from any other pre-Oligocene rocks in North

America. This fact, along with the poor nature of the material, leads me to treat this specimen as *Gagaria? salis*. Until additional material is located, there is nothing to add to Cooke's description.

IV. ACKNOWLEDGMENTS

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RODOLFO F.J. BRUNET
PUERTO MADRYN, CHUBUT PROVINCE
ARGENTINA

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I. ABSTRACT

The second part of this work contains the descriptions and systematics of gastropods obtained from the upper levels of the Entrerriense Formation (Late Miocene), outcropping at various localities in the Valdes Peninsula, Chubut Province, Argentina. Herein are treated 62 species, of which 37 are new to science, the remainder are either previously described or closely related to described species. Forty-two species are new to the fauna, which consolidates the affinities with the Panamanian, Caribbean, and Neozelandic Bioprovinces.

II. INTRODUCTION

This paper is a continuation of a previous study examining the molluscan fauna of the Entrerriense Formation (Late Miocene) of the Valdes Peninsula, Chubut Province, Argentina, and with the material contained herein we increase the number of species of Gastropoda recorded in the formation to a total of 128, of which 83 are newly described. With regard to the historical considerations and stratigraphy, the reader is kindly referred to Part I (Brunet, 1995). We continue supporting the relationship of these strata with the upper levels of Paraná, Entre Rios Province, Argentina, reported by Bravard (1858), and consider both synchronous and corresponding to a paleogeographic event not yet elucidated.

III. ACKNOWLEDGMENTS

I wish to thank Tulane University for its help in the publication of this second part, and all the persons who contributed to its realization. I am particularly grateful to Dra. Emily H. Vokes, Tulane University, for her enormous help in preparation of the manuscript and the moral support that she offered to me. I also acknowledge the Centro Nacional Patagónico (CENPAT), which permitted the use of their Servicio Fotográfico, as well as the technical help of Sr. Franciso Pertini.

IV. SYSTEMATIC PALEONTOLOGY

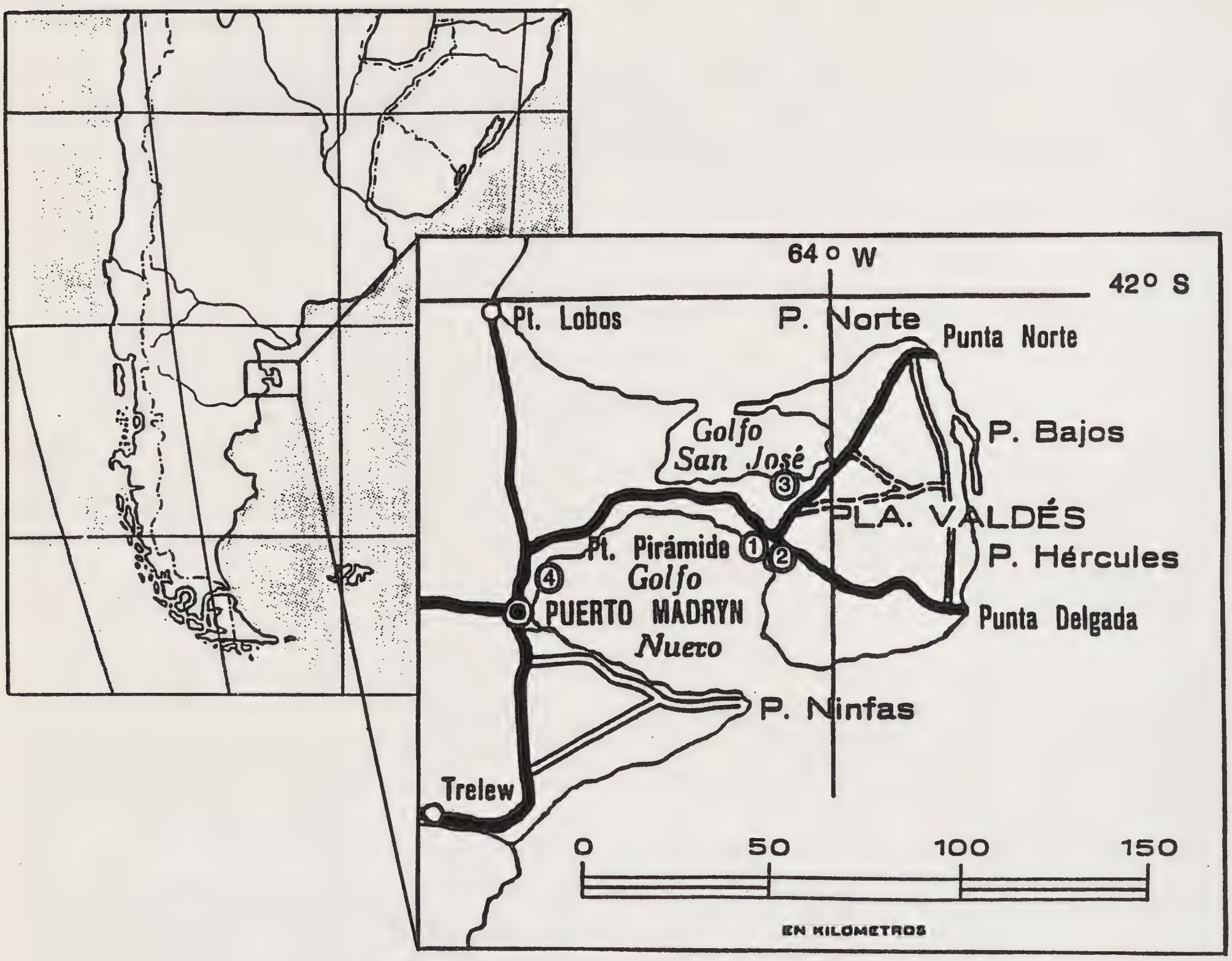
Class GASTROPODA
Order ARCHAEOGASTROPODA
Superfamily PATELLOIDA
Family ACMAEIDAE
Subfamily PECTINODONTINAE
Genus PECTINODONTA Dall, 1882

PECTINDÓNTA sp.
Plate 1, figure 1

Description: Shell coniform, small, curved, low and thin; apex blunt, subcentral, only a bit anterior. Muscle scar in form of a horseshoe with aperture anterior. Ornamented with fine concentric growth lines, in some examples dark concentric bands and fine radial striae, corresponding to original coloration of shell.

Hypotype: MPEF-PI-212; length 10 mm, height 4.1 mm, width 8.1 mm.

Locality: Puerto Piramide, Valdes Peninsula, Chubut Province, Argentina.



Text-figure 1. Map of Argentina, showing location of Valdes Peninsula. Inset map with fossil localities: 1) Puerto Piramide; 2) Punta Pardela; 3) Playa Fracasso; 4) Baliza Punta Flecha.

Discussion: We assign this example to the genus *Pectinodonta*, because of the low, arcuate shell, with a large blunt apex. Dall (1882) reports *Pectinodonta arcuata* from the Recent of the West Indies. This is the first record of the genus from the Entrerriense Formation of South America.

Family PATELLIDAE
Subfamily NACELLINAE
Genus NACELLA Schumacher, 1817
Subgenus PATINIGERA Dall, 1905
NACELLA (PATINIGERA) aff.
N.(P.) DEAURATA (Gmelin, 1791)
Plate 1, figure 2

Description: Shell relatively thin, oval, slightly elevated. Apex situated on anterior third. Strong radial ribs initially thin at apical level, rapidly becoming wider near margin, other shorter ribs arising at middle of summit, extending to margin; strong concentric cords crossing over ribs, giving to them a tuberculate aspect. Projection of ribs (long and short) producing a scalloped lip. With transmitted light shell showing radiating striae chestnut-yellow in color, corresponding to original coloration of shell.

Hypotype: MPEF-PI-213; length 20.1 mm, height 9.5 mm, width 15.1 mm.

Locality: Puerto Piramide, Valdes Peninsula, Chubut Province, Argentina.

Discussion: The example described presents conchological characters similar to the living species *N.(P.) deaurata*, the caracters differentiating them is the presence of short intercalated ribs between the longer ones and a strong concentric orna-

mentation. The Recent form lives from Latitude 38° South, to the Magellanic region and the Kerguelen Islands. We record this genus and subgenus for the first time from the Entrerriense Formation of South America.

Superfamily TROCHACEA
Family TROCHIDAE
Subfamily MONODONTINAE
Genus TEGULA Lesson, 1835
TEGULA ORBIGNYANA (Pilsbry, 1900)
Plate 1, figure 3

Description: Shell trocoid, with a high spire; five very convex, rounded whorls. Protoconch smooth; sutures very marked; with deep umbilicus. Peristome rounded, thin; columella with three teeth, in some examples only two, the third disappearing. Aperture lacking internal denticles. Ornamented with tuberculated spiral striae, 12 to 13 in number; base with ten to 11 smooth striae, in some examples tuberculated.

Hypotype: MPEF-PI-214; height 7.1 mm, width 10 mm.

Locality: Punta Norte, Valdes Peninsula, Chubut Province, Argentina.

Discussion: Our examples show no differences from specimens living from Mar del Plata to Santa Cruz (Argentina). They probably should be placed in the subgenus *Agathistoma* Olsson and Harbison, 1953. *Tegula patagonica* (d'Orbigny, 1840), which has been cited from the Entrerriense Formation, differs by having denticles on the inner margin of the lip.

Superfamily LITTORINOIDEA
Family LITTORINIDAE
Subfamily LITTORININAE
Genus LITTORINA Ferussac, 1822
LITTORINA aff. L. ZICZAC (Gmelin, 1791)
Plate 1, figures 4-6

Description: Shell small, conical, almost as high as wide, moderately heavy; five or six rather flat whorls (specimens very corroded); suture well marked and smooth. Body-whorl half of total height, very convex, with an obtuse peripheral carina. In some apparently gerontic examples a discontinuous subsutural carina (Bequaert, 1943). First two whorls smooth, sculpture only visible on base, consisting of fine spiral cords. Aperture pyriform; outer lip thin, united directly to body-whorl. Columellar area moderately long and wide, oblique within, smooth, at times rather concave; inner lip rounded, curving gradually toward base; lacking umbilicus.

Hypotypes: MPEF-PI-215; height 11.5 mm, width 11.5 mm (female example). MPEF-PI-216; height 7 mm, width 4 mm (male example). MPEF-PI-217; height 3.8 mm, width 2.2 mm.

Locality: Puerto Piramide, Valdes Peninsula, Chubut Province, Argentina.

Discussion: From the Entrerriense Formation two species have been described as *Littorina unicostalis* Borchert, 1901, and *Littorina paranensis* Borchert, 1901, both from Paraná (Argentina); the first also has been reported from the Camacho Formation of Uruguay (Figueiras and Broggi, 1971-73). The specimen figured here (pl. 1, fig. 4; MPEF-PI-215) possibly represents a female example, in which case the other example (pl. 1, fig. 5; MPEF-PI-216) should be a male, ornamented with fine and coarse spiral cords. We have also observed other examples (pl. 1, fig. 6; MPEF-PI-217) with a very conical form and conspicuous peripheral carina, which resemble those from the area of Governor's Harbour, Eleuthra, Bahama Islands, figured by Bequaert (1943, pl. 5, fig. 5).

LITTORINA SAXATILIS (Olivi, 1792)
Plate 1, figure 7

Description: Shell turbinate, variable in shape, but higher than wide, heavy; three or four whorls increasing rapidly, the last two-thirds of total height, whorls convex; suture deep; without visible ornamentation. Aperture semicircular, outer lip thin, smooth. Columellar area wide, heavy, smooth, expanding toward basal margin and toward body-whorl. A small umbilicus beside columellar margin (juvenile example). Apparently color in this species variable, with yellow, orange, grayish-orange, or grayish-maroon in adults, with one or more spiral bands, white, gray-black, gray, or dark purple. Our specimen with uniform yellowish coloration, with dark purple band in middle of penultimate whorl and another subsutural band on body-whorl, coloration considered to be original color.

Hypotype: MPEF-PI-218; height 5 mm, width 3 mm.

Locality: Puerto Piramide, Valdes Peninsula, Chubut Province, Argentina.

Discussion: Littorina saxatilis occurs in the boreal and arctic areas. In North America it extends from Cape Barrow, Southampton Id., and Hudson's Bay, to southern New Jersey. It also is found in Post-Pliocene deposits that represent brackish lagoons near Branford, Connecticut (Knight, 1934, *in* Bequaert, 1943, p. 10). This is the first record for this species from the Entrerriense Formation of South America, as well as the southernmost record of the species presently known.

LITTORINA PIRAMIDESIA, n. sp.
Plate 1, figure 8

Description: Shell of small size, turriform, heavy, high-spired, whorls convex; body-whorl almost twice height of spire, very globose with

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PLATE 1

Figures Page
1. PECTINODONTA sp. 61
MPEF-PI-212 (hypotype); length 10 mm, height 4.1 mm, width 8.1 mm.
Locality: Puerto Piramide, Valdes Peninsula, Chubut Province, Argentina.
2. NACELLA (PATINIGERA) aff. N.(P.) DEAURATA (Gmelin, 1791) 62
MPEF-PI-213 (hypotype); length 20.1 mm, height 9.5 mm, width 15.1 mm.
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3. TEGULA ORBIGNYANA (Pilsbry, 1900) 63
MPEF-PI-214 (hypotype); height 7.1 mm, width 10 mm.
Locality: Punta Norte, Valdes Peninsula, Chubut Province, Argentina.
4. LITTORINA aff. L. ZICZAC (Gmelin, 1791) (female) 63
MPEF-PI-215 (hypotype); height 11.5 mm, width 11.5 mm.
Locality: Puerto Piramide, Valdes Peninsula, Chubut Province, Argentina.
5. LITTORINA aff. L. ZICZAC (Gmelin, 1791) (male) 63
MPEF-PI-216 (hypotype); height 7 mm, width 4 mm.
Locality: Puerto Piramide, Valdes Peninsula, Chubut Province, Argentina.
6. LITTORINA aff. L. ZICZAC (Gmelin, 1791) 63
MPEF-PI-217 (hypotype); height 3.8 mm, width 2.2 mm.
Locality: Puerto Piramide, Valdes Peninsula, Chubut Province, Argentina.
7. LITTORINA SAXATILIS (Olivi, 1792) 63
MPEF-PI-218 (hypotype); height 5 mm, width 3 mm.
Locality: Puerto Piramide, Valdes Peninsula, Chubut Province, Argentina.
8. LITTORINA PIRAMIDESIA, n. sp. 64
MPEF-PI-219 (holotype); height 7.2 mm, width 4.8 mm.
Locality: Puerto Piramide, Valdes Peninsula, Chubut Province, Argentina.
9. LITTORINA NEBULOSA TESSELLATA Philippi, 1847 66
MPEF-PI-220 (hypotype); height 3.9 mm, width 2.6 mm.
Locality: Puerto Piramide, Valdes Peninsula, Chubut Province, Argentina.
10. VITRINELLA PARDELENSIS, n. sp. 66
MPEF-PI-222 (holotype); height 2 mm, diameter 5.1 mm.
Locality: Punta Pardela, Valdes Peninsula, Chubut Province, Argentina.
11. CIRCULUS PARDELENSIS, n. sp. 66
MPEF-PI-223 (holotype); height 1.3 mm, width 3.1 mm.
Locality: Punta Pardela, Valdes Peninsula, Chubut Province, Argentina.
12. TEINOSTOMA (AEPYSTOMA) aff. T.(A.) ANDRIUM Woodring, 1957 67
MPEF-PI-224 (hypotype); height 2.4 mm, diameter 4 mm.
Locality: Baliza Punta Flecha, Puerto Madryn, Chubut Province, Argentina.
13. CREPIDULA ANCESTRA, n. sp. 74
MPEF-PI-234 (holotype); height 21 mm, width 20.3 mm, diameter 6 mm.
Locality: Puerto Piramide, Valdes Peninsula, Chubut Province, Argentina.
14. CREPIDULA ANCESTRA, n. sp. 74
MPEF-PI-235 (paratype); height 26 mm, width 19.5 mm, diameter 12 mm.
Locality: Puerto Piramide, Valdes Peninsula, Chubut Province, Argentina.

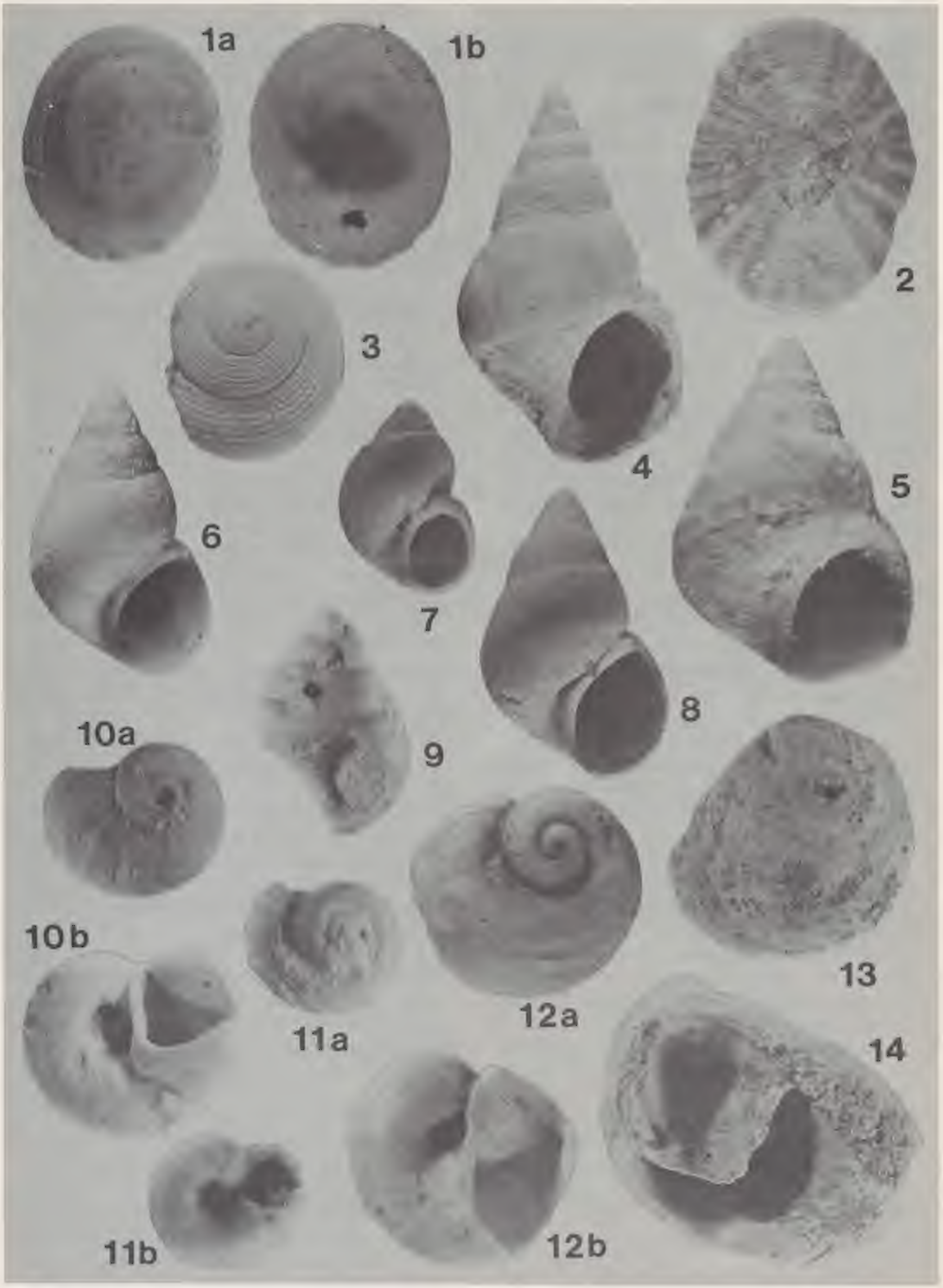

PLATE 1

heavy peripheral carina. Aperture semicircular; outer lip heavy, very curved; columellar area consisting of a heavy callus folded back over body-whorl, beginning within aperture and forming angle with basal lip, which also is wide. Base convex; umbilicus not covered by columellar callus. Although appearing smooth, under microscope (X 40) fine spiral striae present.

Holotype: MPEF-PI-219; height 7.2 mm, width 4.8 mm.

Type locality: Puerto Piramide, Valdes Peninsula, Chubut Province, Argentina.

Derivatio nominis: Named for the type locality.

Discussion: Littorina piramidesia, n. sp., is characterized and differentiated from other related species by the development of the columellar callus, by the very convex whorls, and the constant presence of an umbilicus in juvenile and adult specimens. In apparently female examples, there are microscopic spiral striae, while in male examples the spire is shorter and the ornamentation consists of fine spiral cords.

LITTORINA NEBULOSA TESSELLATA
Philippi, 1847
Plate 1, figure 9

Description: Shell very small; spire conical, low, but pointed; last whorl very globose, without peripheral carina, double or more than height of spire. Suture very marked, shoulder of whorls obtusely anguled by depth of suture. Aperture subcircular, outer lip thin. Columellar area long, wide and smooth, inner lip thickened, almost straight; ending abruptly below, separated by a slight depression in the outer lip. Neither umbilicus nor columellar depression.

Hypotype: MPEF-PI-220; height 3.9 mm, width 2.6 mm.

Locality: Puerto Piramide, Valdes Peninsula, Chubut Province, Argentina.

Discussion: We assign this example to the variety *tessellata* because of the angulation of the shoulder and the very globose body-whorl. This is the first record from the Entrerriense Formation of South America.

Family VITRINELLIDAE
Genus VITRINELLA C.B. Adams, 1850

VITRINELLA PARDELENSIS, n. sp.
Plate 1, figure 10

Description: Shell of small size, porcelaneous, compressed, smooth, widely umbilicate, diameter of shell 5.1 times diameter of umbilicus. Three and one-half convex whorls, the last inferiorly flat. Aperture strongly oblique, basal outline subrectangular due to superior extension of peristome, inferior retraction and parallel nature of the columellar and outer margins. Columellar margin folded back over whorl, extending to umbilicus, but not obscuring it. Ornamented with heavy growth lines.

Holotype: MPEF-PI-222; height 2 mm, diameter 5.1 mm, diameter of umbilicus 1 mm.

Type locality: Punta Pardela, Valdes Peninsula, Chubut Province, Argentina.

Derivatio nominis: Named for the type locality.

Discussion: Vitrinella pardelensis, n. sp., is rather similar to *V. floridiana* Pilsbry and McGinty, 1946, which differs in having a proportionally larger umbilicus, an aperture that is oblique but not typically "teinostomiform" as in *V. pardelensis*. The columellar margin does not cover the basal whorl and the the aspect of the aperture laterally is rounded and basally subtriangular. *Vitrinella helicoidea* C.B. Adams, 1850, differs in having a parietal division of the lip into which penetrates the penultimate whorl, heavy periumbilical carina and the upper margin of the peristome is curved forward; the diameter of the shell is 3.3 times the diameter of the umbilicus. *Vitrinella praecox* Pilsbry and McGinty, 1946, differs by having a periumbilical carina, a peristome oblique but not "teinostomiform" and the diameter of the shell is 3.75 times the diameter of the umbilicus. We note for the first time this genus from the Entrerriense Formation of South America.

Genus CIRCULUS Jeffreys, 1865
CIRCULUS PARDELENSIS, n. sp.
Plate 1, figure 11

Description: Shell very small, heavy, spire moderately low, exposed, peripherially rounded. Suture weakly marked, with a wide parasutural groove beginning at protoconch and having six to eight poorly developed fine spiral striae. Protoconch smooth; penultimate whorl ornamented with five heavy spiral cords and ulti-

mate with 12 heavy cords. Aperture oblique, subquadrate, with extended upper lip, the lower and upper almost straight, the outer barely convex. Umbilicus very deep, with strong periumbilical growth lines only.

Holotype: MPEF-PI-223; height 1.3 mm, width 3.1 mm.

Type locality: Punta Pardela, Valdes Peninsula, Chubut Province, Argentina.

Derivatio nominis: Named for the type locality.

Discussion: Relatively near living forms are known from the Atlantic and the Pacific. *Circulus trilix* (Bush, 1897) ranges from Cape Hatteras to Cuba, and is distinguished by being tricarinate and lacking the parasutural groove. Woodring (1957) cites this species from the Chipola (Early Miocene), Shoal River (Middle Miocene), and Gatun (Late Miocene) formations; also with tricarinate forms. *Circulus cerrosensis* Bartsch, 1907, from Santa Catalina Island, California, Baja California, and the Gulf of California, may be considered the Pacific homologue of *C. trilix*. *Cyclostremiscus glyptomphalus* Pilsbry and Olsson, 1952, from the Pleistocene of Panama, may be distinguished with difficulty from *C. trilix*; therefore, those authors suggested the existence of a "race" or a subspecies. *Circulus cosmius* Bartsch, 1907, from Ecuador is rather near *C. cerroensis*, but is characterized by a narrow curvature of the upper margin of the peristome, directed downward, extending forward, lacking the parasutural groove. *Circulus occidentalis* Pilsbry and Olsson, 1941, from the Pliocene of Ecuador, has the margin of the peristome directed below, lacks the parasutural groove and resembles *C. cosmius*. *Circulus philippii* (Cantraine, 1842) also has a deep umbilicus, is ornamented with a much greater number of spiral cords and lacks the parasutural groove.

Genus TEINOSTOMA H. Adams and A. Adams, 1854
Subgenus AEPYSTOMA Woodring, 1957
TEINOSTOMA (AEPYSTOMA) aff. T.(A.) ANDRIUM Woodring, 1957
Plate 1, figure 12

Description: Shell of small size, heavy, convex, with three and one-half whorls, spire somewhat elevated, last whorl very large. Protoconch smooth. Peristome typical, with upper margin projecting forward and lower withdrawn. Umbilicus open, on the basis of an immature example, with slight development of a callus. Sculture of spiral cords crossed by radiating cords, creating a cancellate ornamentation over entire surface.

Hypotype: MPEF-PI-224; height 2.4 mm, diameter 4 mm.

Locality: Baliza Punta Flecha, Puerto Madryn, Chubut Province, Argentina.

Discussion: This form presents characters very similar to the holotype of Woodring (1957, p. 70, pl. 18, figs. 9-11), which also is an immature example. The dimensions of the holotype are: height 2 mm, diameter 4.7 mm. This is the first record for the genus *Teinostoma* and the subgenus *Aepystoma* from the Entrerriense Formation of South America.

Superfamily CERITHIOIDEA
Family TURRITELLIDAE
Genus TURRITELLA Lamarck, 1799
TURRITELLA HEIMI, n. sp.
Plate 2, figure 1

Description: Shell turriculate, of medium size. Six and one-half teleoconch whorls, with two smooth nepionic whorls. Suture deep and shoulder very marked. Whorls flat. First teleoconch whorl with four cords, the remaining with five, consisting of one strong anterior and one strong posterior, with three weaker intermediate cords, between each of these a very fine secondary cord; behind the posterior and bordering the shoulder one fine cord and, in advance of the anterior, another fine cord. Suture with a secondary cord above and another below. In adult examples, upper and infrasutural cords disappearing and on last whorls two or three very fine cords between primaries. Heavy growth lines causing some cords to appear tuberculate, especially the primaries. Base with a heavy peripheral cord and four low flat cords, between these one or two fine secondary cords. Aperture apparently oval, with a thin columellar border, columella convex. Growth lines typical of *T. conspicabilis* (Miocene of Australia) and of the *T. hybrida* group (Cretaceous-Eocene of Europe), according to Guillaume (1924).

Holotype: MPEF-PI-225; height 18.1 mm, width 5.8 mm, apical angle 16°.

Type locality: Puerto Piramide, Valdes Peninsula, Chubut Province, Argentina.

Derivatio nominis: Dedicated to the late geologist Dr. Arnoldo Heim.

Discussion: Turritella heimi, n. sp., differs from *T. americana* (Bravard, 1858), which has only four primary cords per whorl and one irregular fine cord on the early whorls, while on the last whorl there may be intercalated up to two intermediate cords, all cords with granulations, over the early teleoconch whorls. *Turritella iheringiana* Figueiras and Broggi, 1976, differs in having each whorl with seven subequal cords, except the upper, which is stronger and peripheral to the shoulder. The sutural area lacks cords and the base has five flat cords. *Turritella indeterminata* Borchert, 1901, differs in having convex whorls, with nine cords, and with finer secondary cords.

TURRITELLA BROGGII, n. sp.
Plate 2, figure 2

Description: Shell turriform, of medium size, whorls flat, suture inconspicuous, without either sutural depression or shoulder. Twelve and one-half whorls, two smooth nepionic whorls; first teleoconch whorls with three smooth, irregular cords, the remaining with three primary cords, somewhat heavy, equal and granulose; on last whorl one anterior cord added, also granulose and corresponding to periphero-basal cord; between each pair of principal cords one fine, low secondary cord with small granules. Base with a heavy peripheral cord and five flatter cords, with one secondary cord between each of them. Columella straight and aperture subquadrate; no growth lines seen on any specimens.

Holotype: MPEF-PI-226; height 20 mm, width 6 mm, apical angle 19°.

Type locality: Puerto Piramide, Valdes Peninsula, Chubut Province, Argentina.

Derivatio nominis: Dedicated to the malacologist Sr. Jorge Broggi.

Discussion: Turritella broggii, n. sp., differs from *T. americana* (Bravard, 1858), which has four granulose primary cords per whorl and an inconsistant fine cord on the first whorls, while on the last whorl there may be intercalated up to two intermediate cords, also with granulations. *Turritella iheringia* Figueiras and Broggi, 1976, has seven cords per whorl, with the upper strongest and forming the shoulder; the base has five flat cords and the suture is within a deep groove. *Turritella indeterminata* Borchet, 1901, has convex whorls, the suture within a deep groove, with nine cords and finer secondaries. *Turritella heimi*, n. sp., has five principal cords, the anterior and the posterior stronger, and an intermediary secondary cord; the suture is within a deep groove, with one suprasutural cord and one infrasutural cord.

TURRITELLA FIGUEIRASI, n. sp.
Plate 2, figure 3

Description: Shell of medium size, whorls flat, suture within a deep groove, shoulder conspicuous. Ornamented with three very heavy cords, barely granulose, and one cord of equal strength in front of anterior suture; in front of this, three fine secondary cords, situated within suture; between anterior suture and cord situated in advance of it, two fine secondary cords; between anterior suture and the middle, one fine low central cord and four very fine cords on each side; between the middle and posterior suture, one fine central cord and three very fine cords on either side; above posterior suture, on shoulder, three or four fine cords, with some of these heavier than others. Base with one heavy peripheral cord and four flat cords, with three to six extremely fine secondary cords between these. Columella straight and aperture subquadrate. No growth lines seen on any specimens.

Holotype: MPEF-PI-227; height 24 mm; width 7.9 mm, apical angle 15°.

Type locality: Puerto Piramide, Valdes Peninsula, Chubut Province, Argentina.

Derivatio nominis: Dedicated to the late paleontologist Dr. Alfredo Figueiras.

Discussion: Turritella figueirasi, n. sp., differs from *T. americana* (Bravard, 1858), which has four granulose cords with two intermediary cords intercalated. *Turritella indeterminata* Borchert, 1901, has strongly convex whorls, nine cords on each whorl, which increase in number on the body-whorl, with one secondary cord intercalated between the primaries. We have no information on the aperture of this species. *Turritella iheringiana* Figueiras

and Broggi, 1976, has seven subequal spiral cords, with the uppermost strongest; the base with five cords, and an apical angle of 20°. *Turritella broggii*, n. sp., has three primary cords, without a suprasutural cord, a distinct number of secondary cords, the base with five primary cords, a single secondary cord between these; lacking a sutural groove. *Turritella heimi*, n. sp., has five primary cords, with one finer secondary cord between them, one suprasutural cord and another subsutural cord; the base with five primary cords and one or two fine intermediary cords; the aperture is oval with a convex columella.

TURRITELLA FLECHENSIS, n. sp.

Plate 2, figure 4

Description: Shell slender, rather thin, whorls convex, suture shallow, shoulder wide, very oblique and barely concave or straight. Whorls with one heavy anterior cord and one posterior on margin of shoulder, somewhat finer; between these four or five finer cords and between the middle of all cords, three or four much finer tertiary threads; in front of primary anterior cord, one fine cord situated within suture. Shoulder with three or four fine cords. Base with one heavy peripheral cord and six flatter cords; between each of these one finer secondary cord. Growth lines as in *T. conspicabilis* (Miocene of Australia) and the *T. hybrida* group (Cretaceous-Eocene of Europe), following Guillaume (1924).

Holotype: MPEF-PI-228; height 19 mm, width 6 mm, apical angle 16°.

Type locality: Baliza Punta Flecha, Puerto Madryn, Chubut Province, Argentina.

Derivatio nominis: Named for the type locality.

Discussion: Turritella flechensis, n. sp., differs from *T. indeterminata* Borchert, 1901, which has three spiral cords on the upper part of the whorl, these followed by six even stronger, on the last whorl even more numerous; aperture not seen in the holotype. *Turritella gatunensis gatunensis* Conrad, 1857, has two primary cords, one in the middle of the whorl and another on the anterior third or quarter, with numerous secondary cords, and with other extremely fine threads, observable under a microscope on the last whorl; the base with numerous fine spiral cords. In the figures of Woodring (1957, pl. 83, figs. 4, 5, 9, 14) there are two or three heavy cords located on the anterior half of the whorls. *Turritella gatunesis rhytodes* Woodring, 1957, has the last whorls very compressed posteriorly, without a well-defined shoulder, approximately 16 to 18 cords covering the entire whorl, from suture to suture, of these three or four most pronounced. *Turritella adela* Woodring, 1957, has approximately nine primary cords of various strength and very fine secondary intermediate cords. *Turritella mataracana* Hodson, 1926, has numerous cords that run from suture to suture, without a well-defined shoulder and with very deep sutures.

TURRITELLA HODSONI, n. sp.

Plate 2, figure 5

Description: Shell slender, with sutures barely visible; protoconch broken; first preserved whorls with three cords, the posterior very heavy, the medial of the strength of the posterior and the anterior somewhat more salient and appressed to suture, at times almost covering it. On last whorls posterior cord becoming flattened, the surface becoming concave, carrying in this concavity one fine cord; anteriorly continuing with median cord, followed by another concavity and finally the conspicuous anterior cord, projecting as a ledge over shallow suture. Aperture presumably suboval, with columella very concave and outer lip with a depression caused by projection of external groove. Apparently base with one heavy, almost flat, peripheral cord.

Holotype: MPEF-PI-229; height 29 mm, width 9.8 mm.

Type locality: Puerto Piramide, Valdes Peninsula, Chubut Province, Argentina.

Derivatio nominis: Dedicated to the late paleontologist Dr. Floyd Hodson.

Discussion: Turritella hodsoni, n. sp., is rather similar to *T. montanitensis* Hodson, 1926, from the Oligo-Miocene of Venezuela, especially the paratype illustrated by Hodson (1926, pl. 16, fig. 6), which differs from our holotype by having a submedial cord on the early teleoconch whorls, in the form of a smooth "V", with one anterior cord and another posterior one, markedly granulose, due to the growth lines and fine intermediate cords,

the secondaries also granulose. *Turritella montanitensis olcotti* Hodson, 1926, has cords with a lesser number of granules, but more conspicuous, especially on supra-sutural cord. *Turritella montanitenesis saladilloensis* Hodson, 1926, has the space between the primary anterior cord and the primary posterior cord more concave, the

PLATE 2

Figures Page

1. TURRITELLA HEIMI, n. sp. 67
MPEF-PI-225 (holotype); height 18.1 mm, width 5.8 mm.
Locality: Puerto Piramide, Valdes Peninsula, Chubut Province, Argentina.
2. TURRITELLA BROGGII, n. sp. 68
MPEF-PI-226 (holotype); height 20 mm, width 6 mm.
Locality: Puerto Piramide, Valdes Peninsula, Chubut Province, Argentina.
3. TURRITELLA FIGUEIRASI, n. sp. 68
MPEF-PI-227 (holotype); height 24 mm, width 7.9 mm.
Locality: Puerto Piramide, Valdes Peninsula, Chubut Province, Argentina.
4. TURRITELLA FLECHENSIS, n. sp. 69
MPEF-PI-228 (holotype); height 19 mm, width 6 mm.
Locality: Baliza Punta Flecha, Puerto Madryn, Chubut Province, Argentina.
5. TURRITELLA HODSONI, n. sp. 69
MPEF-PI-229 (holotype); height 29 mm, width 9.8 mm.
Locality: Puerto Piramide, Valdes Peninsula, Chubut Province, Argentina.
6. TURRITELLA PIRAMIDESIA, n. sp. 72
MPEF-PI-230 (holotype); height 16 mm, width 6.1 mm.
Locality: Puerto Piramide, Valdes Peninsula, Chubut Province, Argentina.
7. TURRITELLA ALZOLAI, n. sp. 72
MPEF-PI-231 (holotype); height 20.1 mm, width 7 mm.
Locality: Puerto Piramide, Valdes Peninsula, Chubut Province, Argentina.
8. SPIROCOLPUS FERUGLIOI, n. sp. 73
MPEF-PI-232 (holotype); height 18.6 mm, width 12 mm.
Locality: Punta Pardela, Valdes Peninsula, Chubut Province, Argentina.
9. PETALOCONCHUS sp. 73
MPEF-PI-233 (hypotype); height 6 mm, width 3.8 mm.
Locality: Baliza Punta Flecha, Puerto Madryn, Chubut Province, Argentina.
10. HIPPONIX FLECHENSIS, n. sp. 73
MPEF-PI-236 (holotype); height 1.8 mm, length 4 mm, width 3.9 mm.
Locality: Baliza Punta Flecha, Puerto Madryn, Chubut Province, Argentina.
11. CAPULUS PIRAMIDENSIS, n. sp. 74
MPEF-PI-235 (holotype); height 3 mm, length 6 mm, width 6 mm.
Locality: Puerto Piramide, Valdes Peninsula, Chubut Province, Argentina.
12. POLINICES (EUSPIRA) CONSIMILIS (Ihering, 1897) 75
MPEF-PI-237 (hypotype); height 7 mm, width 8.5 mm.
Locality: Puerto Piramide, Valdes Peninsula, Chubut Province, Argentina.
13. POLINICES (EUSPIRA) ORTMANNI (Ihering, 1907) 75
MPEF-PI-238 (hypotype); height 9 mm, width 7.2 mm.
Locality: Puerto Piramide, Valdes Peninsula, Chubut Province, Argentina.
14. ATAXOCERITHIUM PARDELENSIS, n. sp. 75
MPEF-PI-239 (holotype); height 9.1 mm, width 4 mm.
Locality: Punta Pardela, Valdes Peninsula, Chubut Province, Argentina.
15. ATAXOCERITHIUM PIRAMIDENSIS, n. sp. 76
MPEF-PI-240 (holotype); height 18.6 mm, width 7 mm.
Locality: Puerto Piramide, Valdes Peninsula, Chubut Province, Argentina.
16. BALCIS FLECHENSIS, n. sp. 76
MPEF-PI-241 (holotype); height 6 mm, width 2 mm.
Locality: Baliza Punta Flecha, Puerto Madryn, Chubut Province, Argentina.

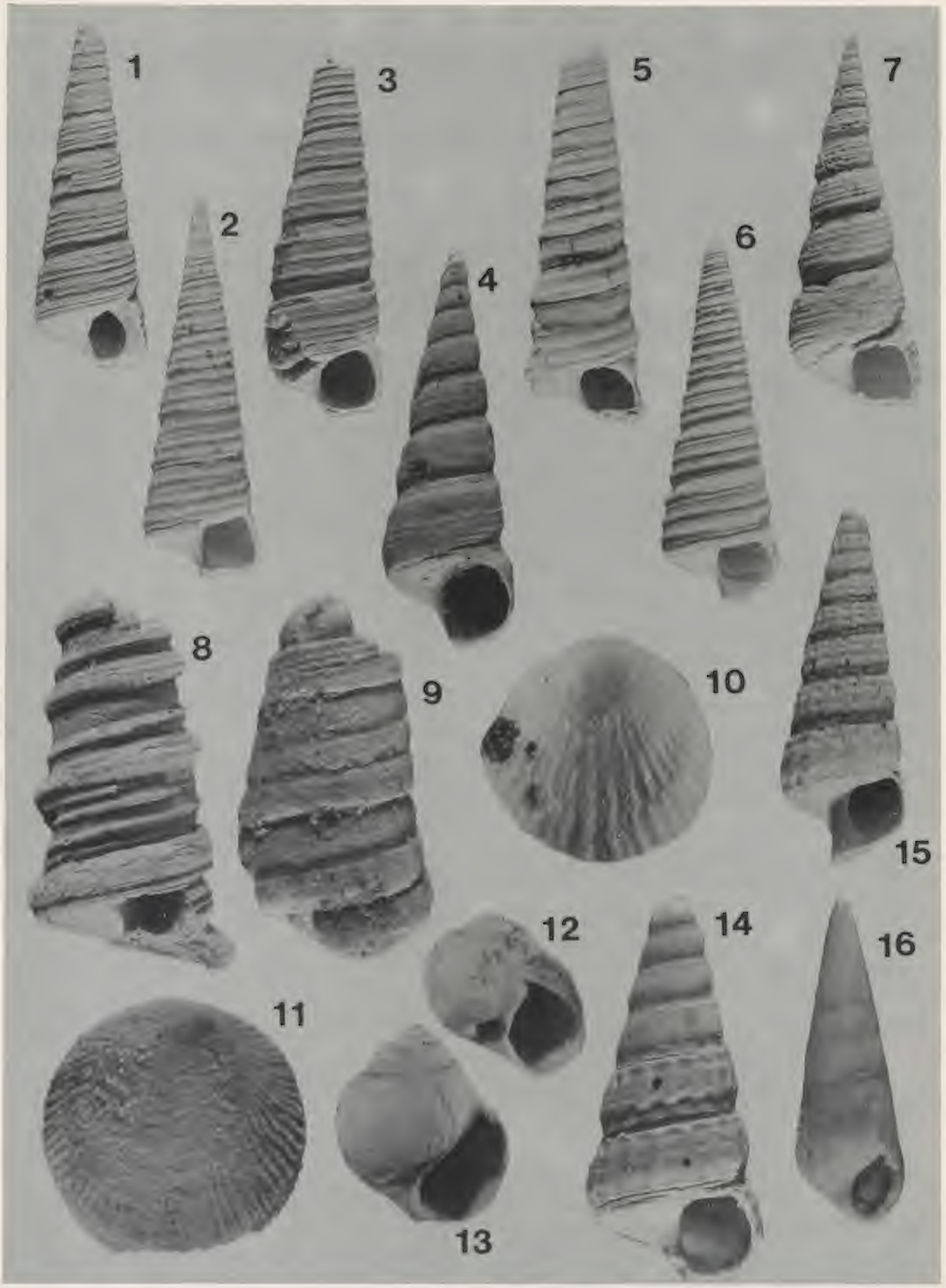

PLATE 2

primary posterior cord weaker, the second primary cord heavier and the two anterior primaries joined. Observing the figures of Hodson, we have some doubt that the example figured as a paratype of *T. montanitensis* (Hodson, 1926, pl. 16, fig. 6) is the same species, we believe that it is referable to another species of *Turritella*, somewhat similar to *T. hodsoni* n. sp., but distinguished from it by the presence of a surface oblique and straight above the anterior cord, while that of *T. hodsoni* is completely concave.

TURRITELLA PIRAMIDESIA, n. sp.
Plate 2, figure 6

Description: Shell of medium size, heavy and slender; eight and one-half flat whorls, two smooth nepionic whorls, suture not visible; shoulder well marked by a granulose posterior cord. Early teleoconch whorls with three spiral cords, the central twice the width of other two and the posterior granulose, with one fine cord occupying the space of the suture; cords increasing in number up to five, one of these becoming heaviest. In more adult whorls, between principal cords finer smooth secondary cords intercalated, up to five in number, one of these always becoming heavier. Principal cords following, the posterior and the median, becoming granulose, but anterior one smooth. Base with one peripheral cord and seven low, convex cords with one fine secondary cord between each of these. Columella curved and aperture oval. No growth lines visible.

Holotype: MPEF-PI-230; height 16 mm, width 6.1 mm.

Type locality: Puerto Piramide, Valdes Peninsula, Chubut Province, Argentina.

Derivatio nominis: Named for the type locality.

Discussion: Turritella piramidesia, n. sp., differs from *T. broggii*, n. sp., which has a less well-marked shoulder, three equal granulose cords, with a fourth cord intercalated on the last whorl, and only one fine granulose secondary cord, which is intercalated between the primaries; the columella is straight and the aperture subquadrate. *Turritella heimi*, n. sp., has four cords on the early teleoconch whorls and five primary cords on the last whorls, with one anterior cord and another heavy posterior one and three finer intermediate cords; in the suture there are only two cords, one suprasutural and the other infrasutural. On the base there is one peripheral cord and four additional cords, with one or two secondaries between them.

TURRITELLA ALZOLAI, n. sp.
Plate 2, figure 7

Description: Shell turriform, of medium size. Ten and one-half whorls, with two smooth nepionic whorls. Suture deep, shoulder well-marked and oblique, with whorls very convex. First teleoconch whorls with three primary cords and one secondary cord between them, the middle primary heavier and projecting; later whorls with five primary cords, intercalated between these one to three secondary cords. At level of sutural groove three or four suprasutural cords, the second of these heavier, and one fine cord situated at crest of shoulder of whorl. Base with six doubled, flat cords. Columella convex, with heavy columellar callus covering one-third of base. Aperture subquadrate.

Holotype: MPEF-PI-231; height 20.1 mm, width 7 mm.

Type locality: Puerto Piramide, Valdes Peninsula, Chubut Province, Argentina.

Derivatio nominis: Dedicated to Dr. Rodolfo Mendez Alzola.

Discussion: Turritella alzolai, n. sp., differs from *T. gatunensis gatunesis* Conrad, 1857 (in Woodring, 1957, pl. 23, figs. 4, 5, 9, 14), which has the whorls more compressed posteriorly, causing the shoulder to be less well defined, with only two primary cords and numerous secondary cords, the primaries diminishing in strength on the last whorls; the base is sculptured with fine spiral cords. *Turritella gatunensis rhytodes* Woodring, 1957, has the whorls more compressed posteriorly, with deeper sutures; in this subspecies one or two of the primary cords tend to increase in size, thus the last whorl has five primary cords and numerous secondary cords on the shoulder of all of the whorls, which always reach the suture. *Turritella flechensis*, n. sp., has one heavy anterior cord and one heavy posterior one, with three or four fine secondary cords and between these three or four very fine tertiary cords. The shoulder has three or four fine cords and the base

has six flat cords and one fine intermediate cord. The columella is more convex and lacks a columellar callus.

Genus SPIROCOLPUS Finlay, 1927

SPIROCOLPUS FERUGLIOI, n. sp.

Plate 2, figure 8

Description: Shell turriform, very heavy, with sutures poorly marked; shoulder conspicuous, straight and rather convex owing to great development of posterior cord. Ornamented with one heavy posterior cord at periphery of shoulder, with conspicuous granulations, this followed by two very fine cords and three cords even finer than posterior one, also granulose, with smooth interspaces, equal in width to cords, except interspace between middle and anterior cords, which is twice width of cords; one fine and apparently smooth suprasutural cord below and poorly defined fine cords at level of surface of shoulder completing ornamentation. Base and columella lacking, as well as early whorls. No growth lines visible.

Holotype: MPEF-PI-232; height 18.6 mm; width 12 mm.

Type locality: Punta Pardela, Valdes Peninsula, Chubut Province, Argentina.

Derivatio nominis: Dedicated to Dr. Egidio Feruglio.

Discussion: Spirocolpus feruglioi, n. sp., differs from *S. ambulacrum* (Sowerby, 1846) and from *S. ambulacrum pyramidesia* (Ihering, 1907), by having one heavy crenulated peripheral cord at the shoulder and only three principal cords, with one fine suprasutural cord and, at the level of the surface of the shoulder, fine spiral cords. *Spirocolpus breantiana* (d'Orbigny, 1847) is more slender, with only three heavy cords, of which only the posterior is generally crenulated. These increase on the last whorls up to six in number; the shoulder is much less conspicuous and the suture deeper. *Spirocolpus iheringi* (Cossmann, 1898) has only three cords, with the posterior stronger, but less conspicuous than in *S. feruglioi*. Evidently this species is closely related to the species of *Spirocolpus* from Patagonia and to the species from the time period of Eocene-Middle Oligocene in New Zealand (Marwick, 1957).

Family VERMETIDAE

Genus PETALOCONCHUS Lamarck, 1799

PETALOCONCHUS sp.

Plate 2, figure 9

Description: Shell with only nepionic whorls and a few teleoconch whorls preserved. Protoconch with two or three smooth whorls, continuing with flat, smooth spiral bands, seven in number. Interior totally concealed by lime.

Hypotype: MPEF-PI-233; height 6 mm, width 3.8 mm.

Locality: Baliza Punta Flecha, Puerto Madryn, Chubut Province, Argentina.

Discussion: Up to this time, we have obtained only two examples of this form. Because of the conchological characters, including the protoconch and part of the teleconch consisting of almost flat bands, apparently without ornamentation, we assign these tentatively to the genus *Petaloconchus*. In this case, this would be the first record of this genus from the Entrerriense Formation of South America.

Superfamily HIPPONICOIDEA
Family HIPPONICIDAE
Genus HIPPONIX Defrance, 1819

HIPPONIX FLECHENSIS, n. sp.

Plate 2, figure 10

Description: Shell in form of a cap, small, thin; apex opistogyre, small, pointed, turned to the left, not extending beyond shell margin. Aperture suborbicular; lip crenulated by projection of ribs. Muscle scar in form of a horseshoe, open anteriorly; with an internal perilabral groove, corresponding to position of fixed disk. Ornamented with 42 heavy radial ribs (2 per mm), with interspaces equal in width to ribs; other shorter ribs intercalated, beginning at middle of height of shell, extending to peristome; heavy growth lines giving an almost cancellate aspect.

Holotype: MPEF-PI-236; height 1.8 mm, length 4 mm, width 3.9 mm.

Type locality: Baliza Punta Flecha, Puerto Madryn, Chubut Province, Argentina.

Derivatio nominis: Named for the type locality.

Discussion: Hipponix flechensis, n. sp., differs from *H. oligocostata* Brunet, 1995, which has 37 radial ribs, without intermediate ribs. The height/width index is 0.54 and the width/length index is 0.85, where-

as in *H. flechensis* these indices are: height/width 0.46 and width/length 0.97. *Hipponix costata* Erdemann and Morra, 1985, from the Patagonian of Santa Cruz (Argentina) has more numerous ribs (approximately 50), without intermediate ribs, and its indices are: height/width 0.23 and width/length 0.89. *Hipponix conicus* (Shumacher, 1817), living in the western Pacific (Fremantle, Australia), has heavier ribs (1 per mm) with very fine interspaces, without intermediate ribs and the length of the shell is 2 cm.

Superfamily CREPIDULOIDEA
Family CREPIDULIDAE
Genus CREPIDULA Lamarck, 1799

CREPIDULA ANCESTRA, n. sp.
Plate 1, figures 13, 14

Description: Shell of medium size, subcircular to oval, low to high. Protoconch curved at an angle of 90°. Apex small, pointed or very strong and blunt, projecting beyond posterior margin. Septum small or very deep, depending on thickness of shell, with a medial longitudinal carina divided into two zones; edge of septum convex, in form of an "S," with a deep notch to the left. Pedal muscle scar semicircular, appressed to right insertion of septum. Ornamented with low, radial ribs, apparently without spines, with interspaces equal in width to ribs and with marked growth lines.

Holotype: MPEF-PI-234; height 21 mm, width 20.3 mm, diameter 6 mm (low form).

Paratype: MPEF-PI-235; height 26 mm, width 19.5 mm, diameter 12 mm (high form).

Type locality: Puerto Piramide, Valdes Peninsula, Chubut Province, Argentina.

Derivatio nominis: Denominated thus for having characters of various species of *Crepidula*.

Discussion: Crepidula ancestra, n. sp., presents characters common to various living species. We consider both forms the same, due to the characteristics of the septum and the presence of the radial ribs. The low form is rather close to *C. dilatata* Lamarck, 1822, with its convex septum, but that has a smooth surface. It resembles *C. aculeata* (Gmelin, 1791), by the surface covered with ribs and the longitudinal carina of the septum, but that has the margin of the septum concave. *Crepidula dilatata* var. *patagonica* d'Orbigny, 1847, has the shell very rounded and the external surface weakly rugose, without conspicuous radial ribs. It differs from *Crepidula unguiformis* Lamarck, 1822, because in spite of its depressed form and its concave septum, it does not have conspicuous ribs nor a longitudinal carina on the septum. We believe that we may consider it a valid ancestor to *C. dilatata* var. *patagonica*. The high form resembles *C. protea* d'Orbigny, 1835, but that has a concave septum and a smooth surface. *Crepidula onyx* Sowerby, 1824, has the septum slightly concave and is smooth exteriorly. From Paraná (Entre Rios) *Crepidula paranensis* Borchert, 1901, has been described from a unique example having an oval form, with a blunt apex, which does not extend beyond the margin; the septum is broken, preventing a valid comparison. Closs (1970) has cited *C. paranensis* and *C. protea* from the Middle Miocene of Brazil. Consequently, this is the first record of the genus in the Entrerriense Formation of Patagonia.

Family CAPULIDAE
Genus CAPULUS Montfort, 1810

CAPULUS PIRAMIDENSIS, n. sp.
Plate 2, figure 11

Description: Shell in form of a cap, small but heavy, apex opistogyre, small, very pointed, not extending beyond margin of shell, protoconch clearly visible. Aperture circular, labrum crenulated by projection of ribs. Muscle-scar in form of horseshoe, open anteriorly. External ornamentation consisting of numerous radial ribs (5 per mm), where these are crossed by growth lines, rugae developed; interspaces more narrow than ribs and crossed by fine growth lines; some ribs divided.

Holotype: MPEF-PI-235; height 3 mm, length 6 mm, width 6 mm.

Type locality: Puerto Piramide, Valdes Peninsula, Chubut Province, Argentina.

Derivatio nominis: Named for the type locality.

Discussion: Capulus piramidensis, n. sp., differs from *C. ladyae* Brunet, 1995, which is lower and less broad, with indices of height/length: 0.42 and width/length: 0.83; while those of *C. piramidensis* are: height/length 0.50 and width/length 1.00. It has five ribs per mm, whereas *C. ladyae*

has three per mm and the apex extends past the labral margin. It is not comparable with *C. compressus* Smith, 1891, living in the Argentine littoral (8.5 x 2.5 x 8 mm), *C. incurvatus* (Gmelin, 1791), living from North Carolina to Brasil (16 x 10 mm), or with *C. hungaricus* (Linne, 1767), living from the coast of Iceland to the Mediterranean Sea (diameter 5 cm), which are much larger species. We may deduce that in the Entrerriense Sea there arose a "race" of *Capulus* of very small size, in contrast to those living in the Atlantic today.

Superfamily NATICOIDEA
Family NATICIDAE
Subfamily POLINICINAE
Genus POLINICES Montfort, 1810
Subgenus EUSPIRA Agassiz, 1838

POLINICES (EUSPIRA) CONSIMILIS
(Ihering, 1897)
Plate 2, figure 12

Description: Shell medium-sized, low-spired, the last whorl large and globose, representing four-fifths of total height; suture strongly channeled, whorls very convex. Aperture occupying three-fourths of body-whorl, semilunar in shape. Columella straight, with an inconspicuous callus and without funicule. Umbilicus deep; peristome narrow. Ornamented only by fine growth lines.

Hypotype: MPEF-PI-237; height 7 mm, width 8.5 mm.

Locality: Puerto Piramide, Valdes Peninsula, Chubut Province, Argentina.

Discussion: Polinices (Euspira) consimilis is relatively abundant in the outcrops at the Valdes Peninsula (Chubut). It has been recorded from sediments of Oligocene age at Los Manantiales, La Cuevas, and Monte Entrance and from the Patagoniense of Golfo San Jorge. Ihering (1897) cited *Natica consimilis* from Monte Leon (Sta. Cruz) and, from Paraná (Entre Rios), Borchert (1901) mentioned *Natica entrerriana*, which we consider a synonym of *P.(E.) consimilis*. This taxon differs from *P.(E.) ortmanni* Ihering, 1907, mentioned from Yegua Quemada and Los Manatiales (Monte Leon Formation, Oligocene), by having a more globose form, a lower spire, a larger aperture, and deeper sutures.

POLINICES (EUSPIRA) ORTMANNI
Ihering, 1907
Plate 2, figure 13

Description: Shell small, somewhat globose, spire relatively high, with 4 1/2 whorls, including nepionic. Suture shallow. Body-whorl occupying 76% of total height. Aperture semilunar, occupying 71% of height of body-whorl; inner lip almost straight, with conspicuous posterior callus,the exterior narrow. Umblicus deep, without funicule. Ornamented with fine growth lines.

Hypotype: MPEF-PI-238; height 9 mm, width 7.2 mm.

Locality: Puerto Piramide, Valdes Peninsula, Chubut Province, Argentina.

Discussion: Polinices (Euspira) ortmanni is relatively common in the outcrops of the Valdes Peninsula, we have collected at various times 38 examples in perfect condition, coming from Punta Pardela and Puerto Piramide principally. *Natica ovoidea* Philippi (Ortmann, 1900, p. 380) is a synonym of *Polinices ortmanni* Ihering, 1907.

Suborder HETEROGLOSSA
Superfamily CERITHIOPSOIDEA
Family CERITHIOPSIDAE
Subfamily CERITHIELLINAE
Genus ATAXOCERITHIUM Tate, 1893

ATAXOCERITHIUM PARDELENSIS, n. sp.
Plate 2, figure 14

Description: Shell small, turriculated and heavy. Spire with 4 1/2 whorls and three smooth nepionic whorls. Sutures marked with deep postsutural groove, superior margin of teleoconch whorls strongly projecting as a result of postsutural groove. The last whorls ornamented with three spiral cords up to penultimate and with four on the ultimate, the second much finer than the others, on both whorls the anterior cord more conspicuous; axial cords from 14 to 17 in number, not reaching suture and forming nodules where they cross spirals. Within suture one fine intrasutural cord. Base slightly convex, almost flat, without ornamentation, except for peripheral basal cord. Columella convex, with evidently siphonal canal short and barely curved. Aperture subquadrate.

Holotype: MPEF-PI-239; height 9.1 mm, width 4 mm.

Type locality: Punta Pardela, Valdes Peninsula, Chubut Province, Argentina.

Derivatio nominis: Named for the type locali-

ty.

Discussion: Ataxocerithium pardelensis, n. sp., differs from *A. juliana* (Ihering, 1907), which has more convex whorls, without the typical postsutural depression of *A. pardelensis*. The type specimen of Ihering's species has a postsutural cord, from 18 to 20 axial cords per whorl and three spiral cords on all of the whorls. *Ataxocerithium trespunta* (Ihering, 1907), from the Patagoniense of Cabo Tres Puntas, has seven spiral cords and 30 axial cords per whorl, the base is ornamented with eight simple cords and it has a straight columella. It differs from *A. pullum* (Philippi, 1845), which lacks the postsutural groove, has two to three cords on the base, whorls always with three spiral cords, seeming on the last whorl not tuberculate, but rectangular.

ATAXOCERITHIUM PIRAMIDENSIS, n. sp.
Plate 2, figure 15

Description: Shell medium-sized, turriform, with 8 1/2 whorls plus two smooth nepionic whorls. Sutures deep, with two fine intrasutural cords. Ornamented with three spiral cords on all whorls and from 18 to 24 axial cords crossing spirals to form tubercules. Base weakly convex, with three fine peripheral cords. Columella convex, with siphonal canal short and oblique. Aperture oval.

Holotype: MPEF-PI-240; height 18.6 mm, width 7 mm.

Type locality: Puerto Piramide, Valdes Peninsula, Chubut Province, Argentina.

Derivatio nominis: Named for the type locality.

Discussion: Ataxocerithium piramidensis, n. sp., differs from *A. juliana* (Ihering, 1907), from the Superpatagoniense of San Julian (Sta. Cruz), which has one fine smooth postsutural cord, from 18 to 20 axial cords per whorl, the whorls very convex and narrow, with deeper sutures and the base smooth. *Ataxocerithium trespunta* (Ihering, 1907), from the middle Patagoniense of Cabo Tres Puntas (Sta. Cruz) has seven spiral cords per whorl and 30 axial cords; the base has eight simple cords; the columella is straight and the aperture subquadrangular. *Ataxocerithium pullum* (Philippi, 1845) has the sutures less deep, the whorls flatter, quadrangular tubercules on the last whorl and only two peripheral basal cords. The genus *Ataxocerithium* is noted here for the first time from the Entrerriense Formation of Argentina. Figueiras and Broggi (1986) cited *Cerithiopsis entrerriensis* from the Camacho Formation of Uruguay, as the unique representative of the genus.

Superfamily EULIMOIDEA
Family EULIMIDAE
Genus BALCIS Leach, 1847

PLATE 3

Figures Page
1. TROPHON LEANZAI, n. sp. 78
MPEF-PI-116 (holotype); height 30.6 mm (incomplete), width 20.7 mm.
Locality: Punta Pardela, Valdes Peninsula, Chubut Province, Argentina.
2. TROPHON HARRINGTONI, n. sp. 78
MPEF-PI-124 (holotype); height 23.9 mm (incomplete), width 19.7 mm.
Locality: Puerto Piramide, Valdes Peninsula, Chubut Province, Argentina.
3. TROPHON PLICATUS var. SANTACRUZENSIS Ihering, 1897 79
MPEF-PI-128 (hypotype); height 38.8 mm (incomplete), width 25 mm.
Locality: Punta Pardela, Valdes Peninsula, Chubut Province, Argentina.
4. TROPHON CONTORTUS, n. sp. 80
MPEF-PI-024 (holotype); height 32.8 mm (incomplete), width 27.2 mm.
Locality: Punta Pardela, Valdes Peninsula, Chubut Province, Argentina.
5. TROPHON RETRORSUM, n. sp. 79
MPEF-PI-180 (holotype); height 58 mm (incomplete), width 44.2 mm.
Locality: Punta Pardela, Valdes Peninsula, Chubut Province, Argentina.
6. "TROPHON" VOKESAE, n. sp. 81
MPEF-PI-019 (holotype); height 50 mm (incomplete), width 38.5 mm.
Locality: Punta Pardela, Valdes Peninsula, Chubut Province, Argentina.

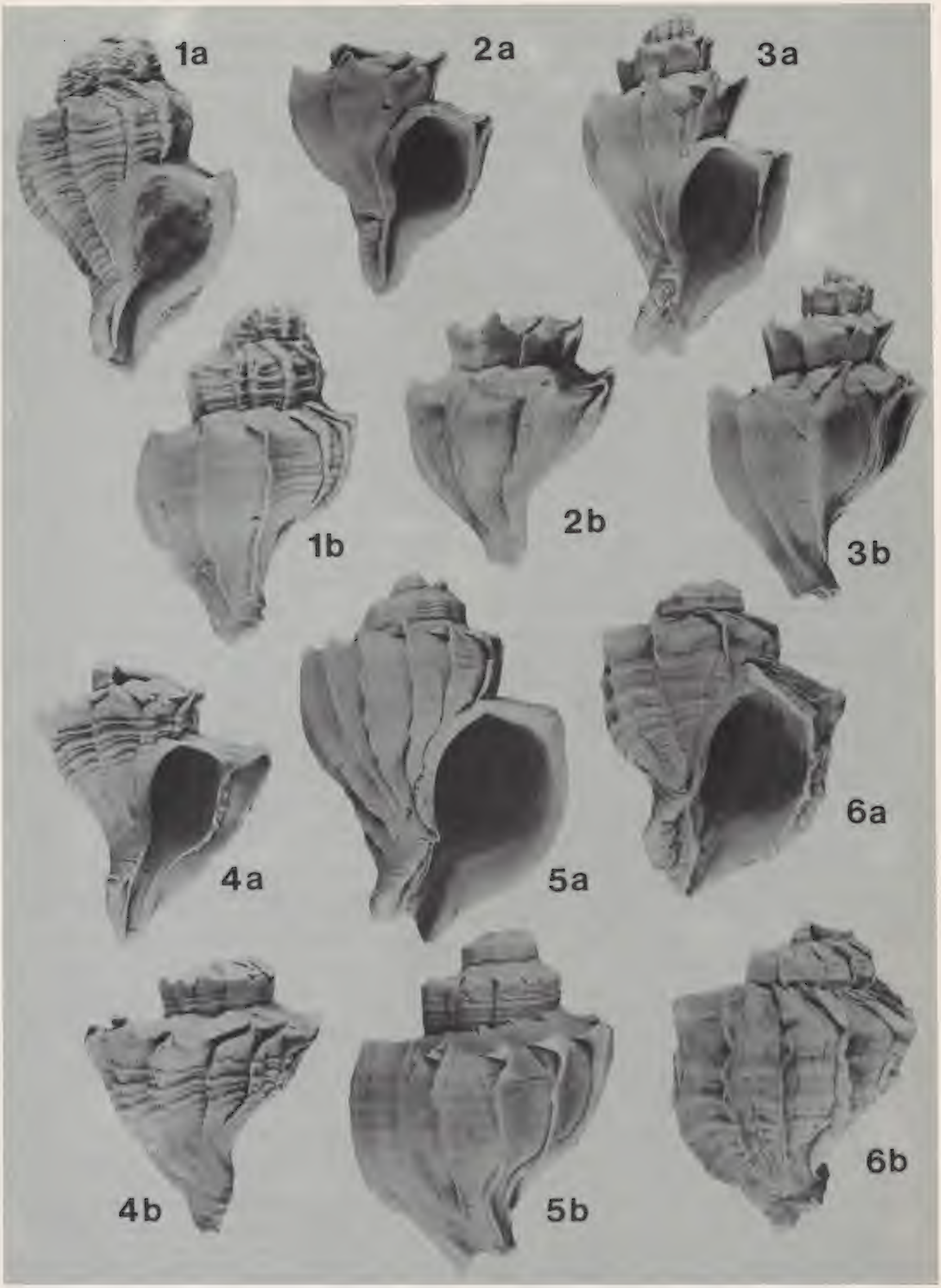

PLATE 3

BALCIS FLECHENSIS, n. sp.
Plate 2, figure 16

Description: Shell very small, slender, 9 1/2 whorls; all almost flat, body-whorl rounded, with strong basal carina; sutures weakly impressed. Aperture oval, external lip broken; columella arched. Without external ornamentation.

Holotype: MPEF-PI-241; height 6 mm, width 2 mm.

Type locality: Baliza Punta Flecha, Puerto Madryn, Chubut Province, Argentina.

Derivatio nominis: Named for the type locality.

Discussion: Balcis flechensis, n. sp., differs from *B. cetia* Woodring, 1970, which has the suture profoundly impressed and very convex whorls. *Balcis aulaca* Woodring, 1970, has very convex whorls, the suture is better marked and there is no peripheral carina on the body-whorl. *Balcis lipara* Woodring, 1970, has somewhat convex whorls, a heavy columellar callus, no peripheral carina on the body-whorl and the two last whorls globose. *Balcis jacululum* (Maury, 1917) has deeper sutures, more convex whorls and lacks a peripheral carina on the body-whorl. This unique example represents the first record of the genus *Balcis* from the Entrerriense Formation of South America.

Superfamily MURICOIDEA
Family MURICIDAE Rafinesque, 1815
Subfamily TROPHONINAE
Cossmann, 1903
Genus TROPHON Montfort, 1810

TROPHON LEANZAI, n. sp.
Plate 3, figure 1

Description: Shell medium-sized, relatively thin. Spire elevated; whorls high and narrow. Aperture subtriangular, with concave columella forming an angle of almost 90 degrees with posterior lip; obtuse posterior angulation; outer lip curved and crenulated. Siphonal canal recurved and long, with umbilicus long and inconspicuous. Fasciole created by growth lines imbricated one above the other. Last whorl with nine relatively strong axial lamellae forming a slightly elevated angulation at shoulder level, continuing up to the suture. Shoulder smooth, at an angle of 45 degrees. Spiral ornamentation consisting of 15 heavy cords with finer alternating ones; one heavy cord forming shoulder of whorl. All heavy intercostal cords prolonged over lamellae, their projection over the edges giving these a crenulated aspect. Axially, between lamellae and crossing cords, from nine to 15 very fine threads. In juvenile examples, axial cords more conspicuous, giving a cancellate appearance.

Holotype: MPEF-PI-116; height 30.6 mm (lacking approximately three whorls), width 20.7 mm. Body-whorl: length 26 mm. Aperture: length 11 mm, width 7.5 mm. Siphonal canal: length 7 mm, width 1 mm.

Type locality: Punta Pardela, Valdes Peninsula, Chubut Province, Argentina.

Derivatio nominis: Dedicated to the late geologist Dr. Armando F. Leanza.

Discussion: Trophon leanzai, n. sp., differs from *T. retrorsum*, n. sp., which has a greater number of lamellae (13) on the body-whorl, lacks the fine spiral cords alternating with the primaries, and has the spire proportionally lower. The siphonal canal is strongly oblique toward the left and the umbilicus forms the parietal margin of the siphonal canal. *Trophon contortus*, n. sp., differs by having a strong constriction at the beginning of the siphonal canal, better development of the lamellae and the lamellar angulations, which turn at the shoulder abruptly in a horizontal direction. The shoulder ramp is wider and horizontal. *Trophon harringtoni*, n. sp., differs in having nine to 11 lamellae, a strong constriction at the beginning of the siphonal canal, faint spiral ornamentation, and lamellar angulations upon reaching the shoulder. The shoulder ramp is broader and horizontal, without lamellar projections, and there is a straight siphonal canal. *Trophon plicatus* var. *santacruzensis* Ihering, 1897, is more similar to *T. plicatus* (Lightfoot, 1786) and thus is not comparable. This species is based on 44 examples.

TROPHON HARRINGTONI, n. sp.
Plate 3, figure 2

Description: Shell small, muriciform, elongated; spire long, composed of six to eight whorls, flattened over suture and nearly vertical on lower part, forming an almost acute angle. Each whorl with nine to eleven projecting axial lamellae, thin at margins, almost straight and

pointed on the angle. Lamellae somewhat varicose and recurved inward, principally on last whorl. Lamellae crossed by fine, regularly marked spiral striae, and barely visible axials. Last whorl twice the height of spire. Peristome somewhat rounded, with margin smooth and folded; siphonal canal narrow and elongated, oblique toward the left, with a narrow and long umbilicus.

Holotype: MPEF-PI-124; height 23.9 mm (lacking approximately three whorls and the protoconch), width 19.7 mm. Aperture: length 11 mm, width 7 mm. Siphonal canal: length 7 mm, width 1 mm.

Type locality: Puerto Piramide, Valdes Peninsula, Chubut Province, Argentina.

Derivato nominis: Dedicated to the late geologist Dr. Horacio Harrington.

Discussion: Trophon harringtoni, n. sp., differs from *T. orbignyi* Carcelles, 1946, which has the spire more elevated and the whorls more narrow; the height/width index of the holotype and 10 paratypes of *T. orbignyi* varies between 1.53 and 2.47, while the indices of the seven examples of *T. harringtoni* vary between 1.21 and 1.32 and apparently the spire does not exceed four whorls. The latter has more developed lamellae, a narrower siphonal canal, oblique to the left. *Trophon plicatus* var. *santacruzensis* Ihering, 1897, from the Early and Middle Patagoniense of Santa Cruz, Argentina, is much smaller in size, with well developed lamellae. The shoulder ramp is flattened, the siphonal canal longer and the umbilicus indefinite. *Trophon retrorsum*, n. sp., has a much larger size, a greater number of varices, and strong spiral ornamentation that produces crenulations on the lamellar margins. The lip is strongly beveled, the siphonal canal very oblique and the umbilicus long and deep. *Trophon contortus*, n. sp., has strong axial lamellae, conspicuous spiral ornamentation that produces strong crenulations on the lamellar margins and a siphonal canal that is longer and curved dorsally. We consider *T. harringtoni* a valid and unique predecessor of *T. orbignyi*.

TROPHON PLICATUS var. SANTACRUZENSIS Ihering, 1897

Plate 3, figure 3

Description: Shell fusiform, heavy, with relatively high spire. Aperture oval with reflected labrum; columella concave with marked callus; siphonal canal wide and oblique. Fasciole formed by imbricated and projecting growth lines; umbilicus poorly defined. Body-whorl with nine laminar varices, strongly angled and curved almost backward to shoulder level; shoulder not flattened. On early whorls marked spiral striae crossing over laminae, later whorls almost smooth.

Hypotype: MPEF-PI-128; height 38.8 mm (lacking protoconch), width 25 mm. Aperture: length 15 mm, width 8 mm. Siphonal canal: length 8.5 mm, width 2 mm.

Locality: Punta Pardela, Valdes Peninsula, Chubut Province, Argentina.

Discussion: Trophon plicatus var. *santacruzensis* differs from *T. plicatus* (Lightfoot, 1786) by having a higher spire, the siphonal canal twisted, more oblique, and wider; with fine spiral striations, very visible on the early whorls and inconspicuous on the body-whorl. The holotype of Ihering's species has 12 varices on the body whorl in contrast to our specimen with only nine. The shoulder is flattened and the siphonal canal is wider. According to Ihering (1907), specimens from Paraná, as well as those from Punta Ninfas and from Golfo Nuevo (Chubut Province), are poorly preserved, making it difficult to assign them to the Entrerriense Formation. Therefore, because of this doubt, we assign this well-preserved specimen to this species.

TROPHON RETRORSUM, n. sp.

Plate 3, figure 5

Description: Shell subfusiform with a short spire, whorls angulose, last whorl triple the height of spire. Aperture oval, with strong postero-external angulation; lip heavy and beveled; strong columellar callus, columella concave posteriorly, ending in one final lamina; siphonal canal broad and short; umbilicus long and deep, turned toward siphonal canal. Ornamentation on last whorl of slightly projecting lamellae, folded over whorl, 13 in number, crossed by inconspicuous spiral cords, alternating heavy and fine, at times doubled, producing crenulations along lamellar margins; lamellae angulated at shoulder level, but elevated only slightly

above it. Subsutural ramp radially wrinkled by growth lines and weak lamellar projections. Penultimate whorl with only five lamellae, all situated on final third of whorl, the remainder with no lamellae, only inconspicuous cords; also on antepenultimate whorl, with latter two whorls having four simple spiral cords.

Holotype: MPEF-PI-180; height 58 mm (only three whorls), width 44.2 mm. Body-whorl: length 50 mm. Aperture: length 24 mm, width 17 mm. Siphonal canal: length 12 mm, width 5 mm.

Type locality: Punta Pardela, Valdes Peninsula, Chubut Province, Argentina.

Derivatio nominis: Denominated thus for the twisted shell.

Discussion: We have observed above the differences between *T. retrorsum*, n. sp., *T. leanzai*, n. sp., and *T. harringtoni*, n. sp. *Trophon retrorsum* differs from *T. contortus*, n. sp., by being of a larger size, with a greater number of lamellae (13) and inconspicuous spiral ornamentation, lacking crenulations on the lamellar margins. The aperture is oval, the siphonal canal very wide and very oblique toward the left, with a conspicuous umbilicus that forms the inner body-whorl wall of the siphonal canal. The differences presented between *Trophon patagonicus* (Sowerby, 1846), from the lower Patagoniense of Santa Cruz (Early Oligocene), *Trophon geversianus* (Pallas, 1774), living on the Patagonian coast, and *Trophon retrorsum*, n. sp., permits us to consider the new species as an intermediate stage between *Trophon patagonicus* and the Recent varieties of *Trophon geversianus*, which is characterized by the presence of more or less well developed lamellae and marked spiral ornamentation or by almost equal development of the lamellae and the spiral ornamentation, such as we observe in the Golfo San Jose, Chubut Province, Argentina (Vokes, 1991B).

TROPHON CONTORTUS, n. sp.
Plate 3, figure 4

Description: Shell small, muriciform; aperture subquadrate; labrum thin with marked crenulations corresponding to projection of spiral cords. Strong prolongation of postero-external labral angle. Siphonal canal long and curved; spire short. The holotype with only 2 1/2 whorls, these somewhat oblique, wider than high, increasing rapidly in diameter, separated by a shallow suture. Ornamentation of last whorl consisting of nine thin lamellae, curved toward peristome, at shoulder of whorl turning abruptly in a horizontal direction; lamellae festoned with five to eight spiral cords passing over them; minor cords intercalated at rate of one between two principal cords; from middle of body-whorl aperturally cords becoming finer, the principal cords disappearing. Shoulder ramp of last whorl practically flat, and extending over it lamellae merging with growth lines, up to level of suture. Besides lamellae, only marked growth lines constituting axial ornamentation. On penultimate whorl, same type of ornamentation, except on shoulder ramp, with three weak spiral cords crossing lamellar projections. Columella curved, with convexity at beginning of siphonal canal, ending in a lamina; fasciole long and narrow, with strong wrinkles.

Holotype: MPEF-PI-024; height 32.8 mm (incomplete), width 27.2 mm. Body-whorl: length 30 mm. Aperture: length 13 mm, width 8 mm. Siphonal canal: length 11 mm.

Type locality: Punta Pardela, Valdes Peninsula, Chubut Province, Argentina.

Derivatio nominis: Denominated thus for the twist of the shell.

Discussion: Trophon contortus, n. sp., differs from *Trophon pelseneri* (Smith, 1915) in having lamellae that do not cross over the shoulder ramp, a wider siphonal canal and less developed lamellae. It differs from *Pagodula vaginatus* (Cristofori and Jan, 1832), which lacks the spiral ornamentation, in being of a much smaller size, having fewer lamellae, axial ornamentation elevated above the shoulder ramp, and the siphonal canal longer and straighter. *Pagodula coulmanensis* (Smith, 1907) has a lesser number of ribs, these being elevated over the shoulder ramp, with less developed spiral ornamentation and a longer and straighter siphonal canal. We have already established the differences between this species and the other species of *Trophon* s.s. described herein.

Genus TROPHON sensu lato

The typical species of *Trophon* have a

medium to large, thin, globose shell, with prominent axial ornamentation. The genus *Xanthochorus* Fischer, 1884, is characterized by a generally low spire, with spiral ornamentation almost equal to or more developed than the axial, with conspicuous tubercules on the intersections. The examples, which are here described as "*Trophon* s.l.", have spiral ornamentation rather similar to *Xanthochorus*, but with strong varices in the manner of the genus *Trophon*.

"TROPHON" VOKESAE, n. sp.
Plate 3, figure 6

Description: Shell muriciform, higher than wide, aperture subtriangular, siphonostomate; lip thin with undulations that correspond to projections of spiral cords; siphonal canal not long and slightly curved toward right. Spire low (in holotype, which lacks two whorls plus protoconch), with whorls wider than high and slightly oblique, enlarging rapidly in diameter; suture somewhat deep and irregular. External ornamentation of strong undulating lamellar processes, ten in number on last whorl. Lamellae 4 to 5 mm in height; in middle of body-whorl forming an angular prolongation reaching to shoulder of whorl; these curving toward right and extending over subsutural ramp up to suture, at this level 2.5 to 4 mm in height. In interlamellar spaces six convex principal cords, the first forming shoulder of whorl; between these from one to three lower convex cords, running spirally. From last primary cord up to fasciole, 12 or 13 low convex cords. On subsutural ramp of body-whorl from three to five barely convex cords. Axial growth lines passing over spiral cords, giving them an undulating aspect. Subsutural ramp oblique downward owing to great development of primary cord delineating it. Penultimate whorl with ten axial laminar processes 2 mm in height, with less marked angulations and four spiral cords; subsutural ramp with growth lines only. Columella slightly curved, ending at level of umbilicus with a heavy laminar process, Umbilicus long but shallow, with a well developed fasciole.

Holotype: MPEF-PI-019; height 50 mm (incomplete), width 38.5 mm. Body-whorl: length 40 mm. Aperture: length 25 mm, width 15 mm.

Type locality: Punta Pardela, Valdes Peninsula, Chubut Province, Argentina.

Derivatio nominis: Dedicated to the paleontologist Dra. Emily H. Vokes of Tulane University, New Orleans, Louisiana (U.S.A.).

Discussion: "Trophon" vokesae, n. sp., differs from *Trophon patagonicus* (Sowerby, 1846) by the greater development of the lamellae, by the greater number of spiral cords, by the lamellar prolongations directed backward, and by the curved siphonal canal. *Trophon geversianus paranaensis* (Borchert, 1901) has less developed axial ornamentation, a smooth lip, and lacks the angular projections on the shoulder, a less developed fasciole and a straight siphonal canal. *Trophon broggii*, n. sp., differs in the weaker development of the lamellae, which are fewer in number (eight), weaker development of the primary spiral ornamentation and a greater number of secondary cords. *"Trophon" piramidensis,* n. sp., has a ficoid form, a low spire, axial ornamentation consisting of eight heavy cords, a homogeneous spiral ornamentation, lacking differentiation between primary and secondary cords. It lacks an umbilicus and has an almost straight siphonal canal. This species is based on 55 adult examples and 73 juveniles.

"TROPHON" BROGGII, n. sp.
Plate 4, figure 1

Description: Shell of medium size, four whorls (lacking the protoconch); aperture oval; labrum broadly projecting toward outer side, with marked undulations formed by projection of spiral cords; strong prolongation of posterio-external angle. Siphonal canal short, barely oblique, recurved upward; spire short, composed of oblique whorls, wider than high, increasing rapidly in diameter, separated by shallow suture. Body-whorl four to five times higher than spire. Ornamentation formed by fine, slightly elevated axial lamellae, eight in number, strongly crenulated, forming a marked angulation on shoulder of whorl; prolonged perpendicularly above subsutural ramp to suture. Subsutural ramp oblique and forming an angle of 110 degrees relative to anterior whorl, the latter ornamented by seven or eight low, flat cords and a heavy cord forming margin of subsutural ramp. Body-whorl with five primary spiral cords, between these from four to seven finer, flat cords, being more numerous (from 20

to 25) from last primary cord to umbilical chink. Lamellae disappearing on two first whorls, being replaced by small axial cords, crossed by from five to eight spiral cords. Columella almost straight, enlarged at beginning of siphonal canal and terminating sharply. Umbilicus long and shallow; strong fasciole with marked folds.

Holotype: MPEF-PI-022; height 66.1 mm (incomplete), width 48 mm; height of spire 12 mm. Body-whorl: length 55 mm. Aperture: length 46 mm, width 16 mm.

Type locality: Punta Pardela, Valdes Peninsula, Chubut Province, Argentina.

Derivatio nominis: Dedicated to Sr. Jorge Broggi, Uruguayan malacologist and paleontologist.

Discussion: "Trophon" broggii, n. sp., differs from *Trophon geversianus paranaensis* (Borchert, 1901), which has a proportionally more developed spire, a smooth lip, no lamellar angulosity at the shoulder, fewer spiral cords (three), and a straight siphonal canal. *Trophon patagonicus* (Sowerby, 1846) has a great number of lamellae (12), with undifferentiated and fewer spiral cords (from three to seven). In the latter, the lamellar angulations are directed upward, but in *Trophon broggii*, n. sp., they are extended laterally. *"Trophon" piramidensis*, n. sp., has a ficoid form, a low spire, axial ornamentation consisting of eight heavy cords, homogeneous spiral ornamentation, lacking differentiation between primary and secondary cords; it lacks an umbilicus and has a straight siphonal canal. Some adults have low varices, others with the varices more or less well developed are similar in appearance to *"T." vokesae*, n. sp., but the juvenile forms of both are easily distinguishable by the greater development of the axial ornamentation in *"T." vokesae*. This species is based upon 39 adult examples and 40 juveniles.

(?)"TROPHON" PIRAMIDENSIS, n. sp.

Plate 4, figure 2

Description: Shell ficoid, broad at level of shoulder of body-whorl, reducing notably its width toward siphonal canal. Spire short, whorls low and globose. Body-whorl constituting approximately 81% of total height (lacking one whorl and the protoconch), globose in posterior part, with shoulder rounded. Aperture subtriangular; columella curved and long; posterior labium concave, at a 90 degree angle to body-whorl; strong posterior angulation; labrum beveled, thin and directed toward outside, with small crenulations corresponding to projection of spiral cords; siphonal canal long, narrow and straight. Fasciole formed by imbricated, barely projecting growth lines, lacking an umbilicus. External ornamentation consisting of eight heavy, projecting axial cords, forming a small, inconspicuous tubercule at shoulder level; these cords lost on anterior third of body-whorl; spirally seven or eight cords above shoulder, and laterally up to 32 flat cords, alternating heavy and weak.

Holotype: MPEF-PI-119; height 28.6 mm (lacking one whorl plus the protoconch), width 19 mm. Aperture: length 15 mm, width 9 mm.

PLATE 4

Figures Page

1. "TROPHON" BROGGII, n. sp. 81
MPEF-PI-022 (holotype); height 66.1 mm (incomplete), width 48 mm.
Locality: Punta Pardela, Valdes Peninsula, Chubut Province, Argentina.
2. (?)"TROPHON" PIRAMIDENSIS, n. sp. 82
MPEF-PI-119 (holotype); height 28.6 mm (incomplete), width 19 mm.
Locality: Puerto Piramide, Valdes Peninsula, Chubut Province, Argentina.
3. FUEGOTROPHON FLINTI, n. sp. 84
MPEF-PI-121 (holotype); height 29.6 mm (incomplete), width 17.5 mm.
Locality: Puerto Piramide, Valdes Peninsula, Chubut Province, Argentina.
4. FUEGOTROPHON TURNERI, n. sp. 84
MPEF-PI-122 (holotype); height 23.5 mm (incomplete), width 16.4 mm.
Locality: Puerto Piramide, Valdes Peninsula, Chubut Province, Argentina.
5. XYMENOPSIS FLECHENSIS, n. sp. 85
MPEF-PI-025 (holotype); height 32.5 mm (incomplete), width 20.5 mm.
Locality: Baliza Punta Flecha, Puerto Madryn, Chubut Province, Argentina.

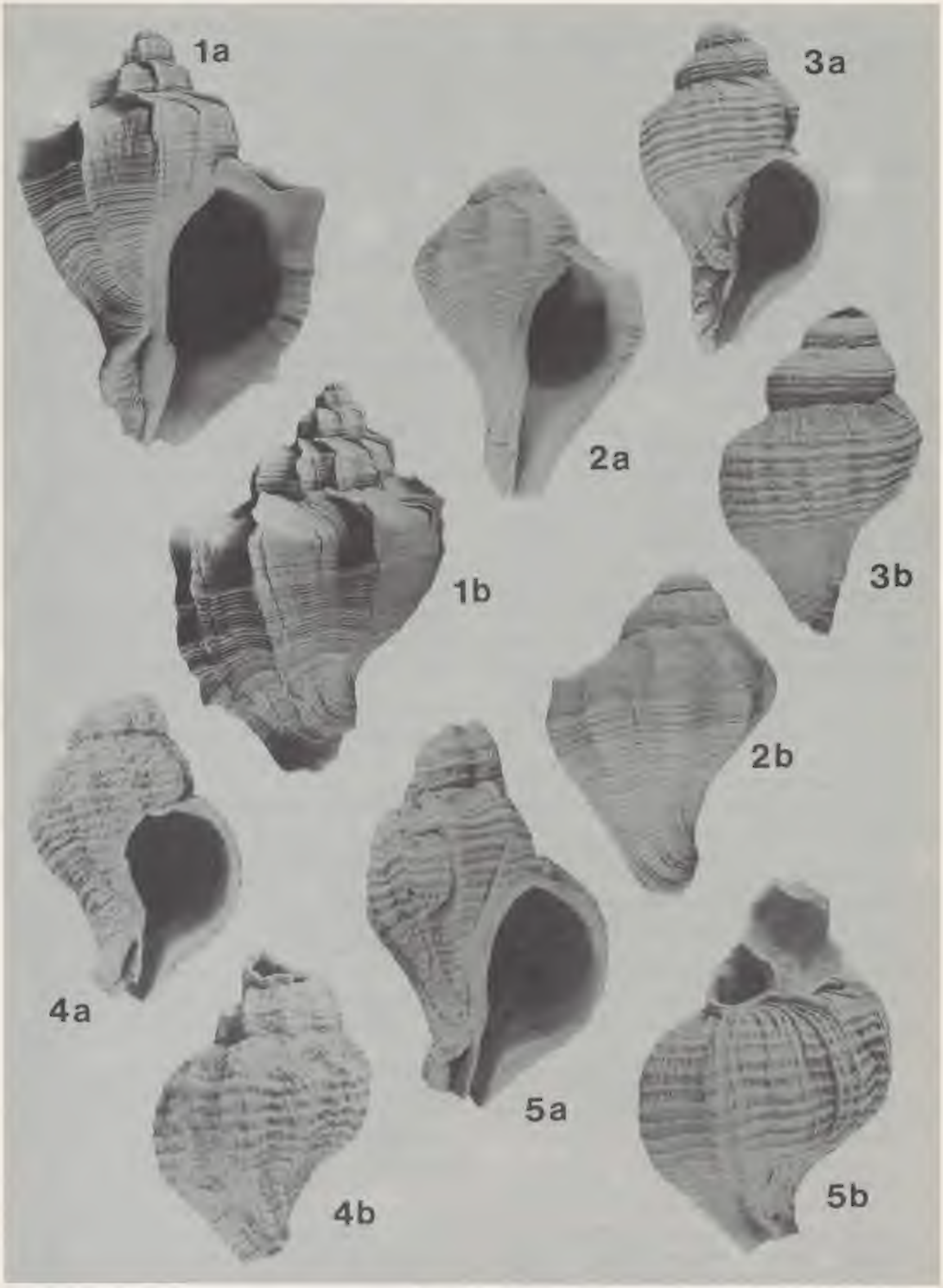

PLATE 4

Siphonal canal: length 6 mm, width 1 mm.

Type locality: Puerto Piramide, Valdes Peninsula, Chubut Province, Argentina.

Derivatio nominis: Named thus for the type locality.

Discussion: (?)"Trophon" piramidensis, n. sp., presents characters atypical of the "muriciforms." It differs from *"T." vokesae*, n. sp., and *"T." broggii*, n. sp., for the reasons expressed in the discussion of each of these. This species is based upon 26 adult examples and 15 juveniles, in some of these there are varices that form a small, acute angulation at the shoulder; in other examples the axial cords are less elevated, but equal in number.

Genus FUEGOTROPHON Powell, 1951

FUEGOTROPHON FLINTI, n. sp.

Plate 4, figure 3

Description: Shell fusiform, spire not elevated; whorls rounded. Aperture pyriform; columella concave posteriorly and convex anteriorly, with well developed columellar callus. Labrum recurved with weak posterior angulation, crenulated along entire margin by projection of spiral cords; siphonal canal long, oblique and relatively wide. Fasciole consisting of imbricated growth lines; no umbilicus. Ornamentation of body-whorl consisting of certain growth lines, more marked than the rest, intercalated as weak axial cords. Spiral cords more developed, four at level of shoulder, one stronger forming shoulder of whorl, and laterally from 16 to 19 spiral cords. Axially innumerable fine, corrugated striae. Penultimate whorl rounded, without shoulder and with nine spiral cords, plus lamelliform axial cordlets.

Holotype: MPEF-PI-121; height 29.6 mm (lacking two whorls, plus the protoconch), width 17.5 mm. Aperture: length 11.5 mm, width 7 mm. Siphonal canal: length 6.5 mm, width 1.5 mm.

Type locality: Puerto Piramide, Valdes Peninsula, Chubut Province, Argentina.

Derivatio nominis: Dedicated to the late geologist Dr. Richard Foster Flint.

Discussion: Fuegotrophon flinti, n. sp., differs from *Fuegotrophon turneri,* n. sp., which has a greater development of the axial ornamentation, consisting of true cords. The subsutural ramp is not differentiated and the aperture is totally rounded, without postero-external angulation. The lip is not beveled and the siphonal canal is oblique. *Fuegotrophon asperum*, n. sp., is fusiform, with the spire more elevated (50% of the total height), and the whorls wider and high. There is one strong cord at the level of the shoulder on the last whorl.

FUEGOTROPHON TURNERI, n. sp.

Plate 4, figure 4

Description: Shell broad and low; last whorl also broad and relatively short. Aperture almost semicircular; labrum rounded with crenulations corresponding to projections of spiral cords. Columella concave; siphonal canal short, narrow, and oblique. Fasciole consisting of imbricated growth lines, umbilicus long but shallow. Body-whorl inflated, with seven heavy, projecting cords; spirally from 16 to 20 cords, crossed by numerous fine, corrugated axial cordlets. Penultimate whorl with only six spiral cords and nine much heavier axial cords.

Holotype: MPEF-PI-122; height 23.5 mm (lacking two whorls and the protoconch), width 16.4 mm. Aperture: length 9.5 mm, width 6.5 mm. Siphonal canal: length 6 mm, width 1 mm.

Type locality: Puerto Piramide, Valdes Peninsula, Chubut Province, Argentina.

Derivatio nominis: Dedicated to the late geologist Dr. Juan C.M. Turner.

Discussion: Fuegotrophon turneri, n. sp., differs from *Fuegotrophon pallidus* (Broderip, 1833) in having a less fusiform shell, a broader spire, a semicircular aperture, a shorter siphonal canal, and by having an umbilicus. It differs from *Fuegotrophon flinti*, n. sp., by having heavier, more marked axial cords, a shorter, oblique siphonal canal, and a conspicuous umbilicus. *Fuegotrophon asperum*, n. sp., is fusiform, with inconspicuous axial ornamentation, but strong spiral ornamentation, and a strong cord forming the shoulder of the body-whorl. It lacks an umbilicus.

FUEGOTROPHON ASPERUM, n. sp.

Plate 5, figure 1

Description: Shell fusiform, small, with six convex whorls, the last almost twice height of spire. Two last whorls with a strong cord forming a shoulder. Aperture oval, with outer lip

beveled and crenulated by projection of spiral cords; siphonal canal narrow, long and oblique. External ornamentation consisting of nine spiral cords, plus two on subsutural ramp; on last whorl four or five poorly defined axial cords. It is not possible to detail other characters of specimen due to incrustation of bryozoans and state of fossilization of shell.

Holotype: MPEF-PI-023; height 18 mm, width 7.9 mm. Body-whorl: length 13 mm. Aperture: length 5 mm, width 3 mm. Siphonal canal: length 3 mm.

Type locality: Puerto Piramide, Valdes Peninsula, Chubut Province, Argentina.

Derivatio nominis: Denominated thus for the roughness of the shell.

Discussion: Fuegotrophon asperum, n. sp., is most similar to the species *Fuegotrophon pallidus* (Broderip, 1833), but differs from it in having a lesser number of spiral cords and in having the aperture represent 62% of the length of the aperture-siphonal canal, whereas in the first species it is 69%. It differs from *F. flinti*, n. sp., and *F. turneri*, n. sp., for the reasons previously discussed under each of these species.

Genus XYMENOPSIS Powell, 1951

XYMENOPSIS FLECHENSIS, n. sp.

Plate 4, figure 5

Description: Shell fusiform, whorls rounded (only 2 1/2 whorls preserved); aperture oval, labrum festooned by projection of spiral cords, siphonal canal rather long and curved; suture shallow and irregular. External ornamentation consisting of eight heavy, wide and rounded, single or double cords, running axially, diminishing in thickness aperturally; from 15 to 17 marked spiral cords, passing over axials; last whorl rounded, with a length more than double that of spire, without forming a shoulder, but axial cords continuing up to suture; penultimate whorl with eleven heavy longitudinal cords, crossed by five finer spiral cords, passing over primaries. Columella slightly concave, ending at canal as a lamina. Umbilicus long, wide and deep; fasciole well developed, with strong folds.

Holotype: MPEF-PI-025; height 32.5 mm (incomplete), width 20.5 mm. Body-whorl: length 28 mm. Aperture: length 14 mm, width 8 mm.

Type locality: Baliza Punta Flecha, Puerto Madryn, Chubut Province, Argentina.

Derivatio nominis: Named for the type locality.

Discussion: Xymenopsis flechensis, n. sp., differs from *Xymenopsis muriciformis* (King and Broderip, 1832) in having fewer axial cords (eight), weaker development of the spiral ornamentation, with a prevalence of the axial ornamentation over the spiral. The aperture with the peristome is much more closed anteriorly, and there is a wide umbilicus. *Xymenopsis falklandicus* (Strebel, 1908) has better development of the spiral ornamentation, a greater number of axial cords and lacks an umbilicus. *Xymenopsis michelii*, n. sp., differs in having lower, wider, more globose whorls. The platform is undifferentiated and the axial ornamentation inconspicuous. The aperture is more elongated, the lip not beveled, the siphonal canal is straight and there is no umbilicus. *Xymenopsis quenseli*, n, sp., has ten strong axial cords, which end in angulations at the level of the shoulder. There is a strong constriction that begins at the siphonal canal. The platform is concave and there is no umbilicus.

XYMENOPSIS MICHELII, n. sp.

Plate 5, figure 2

Description: Elongated shell with rounded whorls, spire high; last whorl representing 81% of total height. External ornamentation consisting of fine axial and spiral cords. Aperture broad, elliptical, with strong columellar callus; labrum rounded with crenulations corresponding to projection of spiral ornamentation; siphonal canal short, wide and slightly curved; fasciolar area consisting of imbricated growth lines and a long but shallow umbilicus.

Holotype: MPEF-PI-118; height 34.2 mm (lacking approximately one whorl plus the protoconch), width 18.8 mm. Aperture: length 11 mm, width 8 mm. Siphonal canal: length 7 mm, width 1.5 mm.

Type locality: Puerto Piramide, Valdes Peninsula, Chubut Province, Argentina.

Derivatio nominis: Dedicated to the diver Sr. Ricardo Micheli.

Discussion: Xymenopsis michelii, n. sp., differs from *X. albidus* (Philippi, 1846) by having a less developed columellar callus and unequal axial ornamentation, without

defined cords. The peristome is not reflected outward, and the crenulations are much less conspicuous. The umbilicus is longer and less deep. *Xymenopsis flechensis*, n. sp., has more globose whorls and more defined axial ornamentation in the form of heavy cords. The aperture is semicircular, the siphonal canal oblique and the umbilicus of greater size. *Xymenopsis quenseli*, n. sp., has the whorls not so globose, with a greater development of the spiral ornamentation and a well defined shoulder. The platform is concave, the axial ornamentation well defined and conspicuous, with on some whorls small angulations at the level of the shoulder. *Xymenopsis peninsularis,* n. sp., has a strong constriction at the beginning of the siphonal canal, ornamentation consisting of strong rounded cords, a deep perisutural groove and a semi-closed siphonal canal.

XYMENOPSIS QUENSELI, n. sp.
Plate 5, figure 3

Description: Shell relatively short and broad, with low whorls. Aperture almost semicircular, with concave columella, posterior lip at a 45 degree angle to body-whorl, with poorly defined posterior angulation, remainder of lip recurved, with crenulations corresponding to projection of spiral cords. Strong constriction at beginning of short, straight, oblique siphonal canal. Fasciole with imbricated growth lines, no umbilicus. Body-whorl ornamented by ten heavy axial cords. Strong spiral ornamentation of 15 to 18 cords, passing over axial cords, alternating between heavy and weak, that forming shoulder heavier. Shoulder oblique, with weak growth lines and two or three weak spiral striae.

Holotype: MPEF-PI-120; height 24 mm (lacking two whorls and the protoconch), width 16.4 mm. Aperture: length 10 mm, width 7.5 mm. Siphonal canal: length 5 mm, width 2 mm.

Type locality: Puerto Piramide, Valdes Peninsula, Chubut Province, Argentina.

Derivatio nominis: Dedicated to the late geologist Dr. Percy Quensel.

Discussion: We have established above the differences between *Xymenopsis quenseli*, n. sp., *X. flechensis*, n. sp., and *X. michelii*, n. sp. *Xymenopsis peninsularis*, n. sp., has more globose whorls, eight axial cords on the body-whorl, with less development of the spiral ornamenation. It lacks the shoulder ramp, which is replaced in this case by a perisutural groove. The siphonal canal is closed at the beginning by a projection of the lip.

XYMENOPSIS PENINSULARIS, n. sp.
Plate 5, figure 4

Description: Shell ficoid, very thin, with short spire and globose whorls. Body-whorl broad at beginning, diminishing rapidly in diameter. Aperture pyriform, columella concave, with a conspicuous columellar callus. Labrum strongly crenulated by projection of external spiral cords; siphonal canal moderately long, closed at beginning by a projection of lip, more open anteriorly. Fasciole composed of imbricated but weakly projecting growth lines. Ornamentation of body-whorl consisting of heavy tuberculate cords beginning at level of suture, eight in number; disappearing in middle of whorl. Five spiral cords on shoulder and from 18 to 20 on lateral face; between these finer threads intercalated. At suture a deep groove bordering all whorls, crossed only by growth striae.

Holotype: MPEF-PI-123; height 20 mm (lacking two whorls and the protoconch), width 14.7 mm. Aperture: length 8 mm, width 5 mm. Siphonal canal: length 6 mm, width 1 mm.

Type locality: Puerto Piramide, Valdes Peninsula, Chubut Province, Argentina.

Derivatio nominis: Dedicated to the Valdes Peninsula, site of the type locality.

Discussion: Xymenopsis peninsularis, n. sp., differs from *X. flechensis*, n. sp., *X. michelii*, n. sp., and *X. quenseli*, n. sp., for the reasons mentioned in the treatment of each of these species. It differs from the living representatives of the genus by the presence of a conspicuous perisutural groove.

Genus PAGODULA Monterosato, 1884
PAGODULA CARCELLESI, n. sp.
Plate 5, figure 5

Description: Shell fusiform, strong; spire high and stepped (approximately 20% of total height); apex with three angular whorls and two nepionic whorls. Aperture subpyriform. Labrum arcuate, corrugated toward outside, with strong posterior angulation. Columellar callus inconspicuous. Siphonal canal long, narrow and open, straight in juvenile examples,

but somewhat curved in adults. Fasciole long, formed by weakly marked imbricate growth lines. Ornamentation consisting of strong, wide lamellae, on body-whorl starting from beginning of siphonal canal, extending separately from body-whorl and upon reaching shoulder becoming markedly elevated and twisted backward. On other whorls, lamellae beginning at suture, running separated from wall of whorl, markedly elevated at level of shoulder and curved backward. Shoulder of whorls showing growth lines in form of an "S," reaching to suture. Well-marked spiral striae on all lamellar surfaces and an axial ornamentation consisting of fine undulating striae, better marked on siphonal canal.

Holotype: MPEF-PI-129; height 57.3 mm (lacking approximately 1/4 of the siphonal canal), width 34.5 mm. Aperture: length 19 mm, width 12 mm. Siphonal canal: length not measurable, width 3.5 mm. Height of lamellae above body-whorl: 6 mm (average).

Type locality: Playa Fracasso, Valdes Peninsula, Chubut Province, Argentina.

Derivatio nominis: Dedicated to the eminent malacologist Alberto Carcelles.

Discussion: Pagodula carcellesi, n. sp., differs from *Padogula carduelis* (Watson, 1883), living in eastern Australia, which has a much smaller size (32 mm; BMNH type collection 87.2.9.571-2), with the spire proportionally higher (29.4% of the total height), and with a greater development of the labral margin and of the postero-lateral angulation. It has strong spiral ornamentation on the early whorls and the columellar callus is more developed. *Pagodula coulmanensis* (E.A. Smith, 1907), living in the Antarctic Zone, has a much smaller size (10.4 mm; BMNH type collection 1905.9.25.02), with fewer lamellae on the body-whorl (six), straight whorls and the shoulder ramp also straight. The spire is proportionally more elevated (39% of total height), the lamellae elevated above the shoulder and the siphonal canal proportionally shorter. This species is based on seven adult examples, in varying states of preservation, collected exclusively from Playa Fracasso over a period of ten years. This is the first record of this genus in the Entrerriense Formation of South America.

PAGODULA aff. P. CARDUELIS (Watson, 1883)
Plate 5, figure 6

Description: Shell muriciform, spire high, whorls slightly rounded. Last whorl with a height of 71% of the total; spire with six whorls; aperture ovoid; columella concave. Labrum beveled and reflected. Siphonal canal long and narrow. Body-whorl ornamented with ten axial lamellae, elevated above the shoulder.

Hypotype: MPEF-PI-125; height 22 mm (only four whorls preserved), width 16.7 mm.

Locality: Puerto Piramide, Valdes Peninsula, Chubut Province, Argentina.

Discussion: Given the state of the shell, which had to be extracted by plastering the shell *in situ*, we assign the species with reservation to *Pagodula carduelis* (Watson, 1883), living off the eastern coast of Australia. We have also studied another two examples, also in a bad state of preservation.

Subfamily THAIDINAE
Genus STRAMONITA Schumacher, 1817

STRAMONITA HOMOGENEUS, n. sp.
Plate 5, figure 7

Description: Shell heavy, oval-oblong, with whorls markedly convex, the last three times the size of the spire; aperture subtriangular; labrum crenulated, crenulations prolonged toward interior of aperture; siphonal canal short and slightly curved; suture shallow. Ornamentation of last whorl provided by axial ribs formed only by growth lines, in places more notable (in some examples forming small nodules on shoulder of whorl). Spiral ornamentation consisting of barely projecting, almost flat cords, from 35 to 45 in number; among these more conspicuous ones forming shoulder of whorl, with two or three more distributed on external face. Growth lines running longitudinally, crossing cords. Penultimate whorl also with weak axial cords and six spiral cords, forming the shoulder. Suture having small oblique folds, forming growth lines upon reaching suture. External lip slightly angulate (very angulate in examples possessing tubercules at shoulder). Columella concave, with post-siphonal thickening forming internal margin of umbilical zone. Umbilicus scarcely suggested; fasciole strong, beginning from parietal lip and forming external rim of umbilical zone.

Holotype: MPEF-PI-026; height 45.7 mm, width 29 mm; height of spire 13 mm. Body-whorl: length 38 mm. Aperture: length 20 mm,

width 12 mm.

Type locality: Punta Pardela, Valdes Peninsula, Chubut Province, Argentina.

Derivatio nominis: Named thus for the inconspicuous ornamentation of the shell.

Discussion: Stramonita homogeneus, n. sp., differs from *Stramonita haemastoma floridiana* (Conrad, 1837) in having an umbilicus, a greater development of the fasciole, and weaker axial ribs. It differs from *Stramonita haemastoma haemastoma* (Linne, 1767) by the absence of tubercules, lacking the palatal sinus and by the presence of an umbilicus. This new species is similar to the subspecies of *Stramonita haemastoma* from Rio de Janeiro and to *Stramonita haemastoma floridiana* from the Florida peninsula. Having obtained a considerable number of specimens permits us to confirm that already in the Tertiary there is a great variability of forms, such as the presence of the umbilicus, although poorly marked, indicating a tendancy toward the disappearance of the same. In the future the reader will be informed on the variability of this species in the Tertiary of Patagonia.

Family NASSARIIDAE

Genus ILYANASSA Stimpson, 1865

ILYANASSA sp.

Plate 6, figure 1

Description: In this unique example there is preserved only part of the last whorl and a small portion of the penultimate. The last whorl apparently wide and strong, the outer lip broken, but it is possible to see lirae interiorly, which end at interior margin of lip. Columella very strong, convex, with one heavy fold at the level of the pillar. Columellar callus very wide, curving over part of wall of body-whorl. Siphonal canal short, deep and oblique toward left. Basal fasciole reaching to middle of body-whorl, with four heavy plications, very projecting and curved. Exteriorly, in spite of wear, appearing to be ornamented with strong axial striae.

Hypotype: MPEF-PI-242; measurement impractical.

Locality: Puerto Piramide, Valdes Peninsula, Chubut Province, Argentina.

Discussion: Ilyanassa sp., in spite of the poor state of preservation, is distinguishable from *I. arata* (Say, 1824), which has a straight siphonal canal, less conspicuous fasciole and spiral ornamentation. *Ilyanassa irrorata* (Conrad, 1863) does not have the heavy columellar plicae and has cancellate ornmentation. *Ilyanassa sex-*

PLATE 5

Figures Page

1. FUEGOTROPHON ASPERUM, n. sp. 84
   MPEF-PI-023 (holotype); height 18 mm, width 7.9 mm.
   Locality: Puerto Piramide, Valdes Peninsula, Chubut Province, Argentina.
2. XYMENOPSIS MICHELII, n. sp. 85
   MPEF-PI-118 (holotype); height 34.2 mm (incomplete), width 18.8 mm.
   Locality: Puerto Piramide, Valdes Peninsula, Chubut Province, Argentina.
3. XYMENOPSIS QUENSELI, n. sp. 86
   MPEF-PI-120 (holotype); height 24 mm (incomplete), width 16.4 mm.
   Locality: Puerto Piramide, Valdes Peninsula, Chubut Province, Argentina.
4. XYMENOPSIS PENINSULARIS, n. sp. 86
   MPEF-PI-123 (holotype); height 20 mm (incomplete), width 14.7 mm.
   Locality: Puerto Piramide, Valdes Peninsula, Chubut Province, Argentina.
5. PAGODULA CARCELLESI, n. sp. 86
   MPEF-PI-129 (holotype); height 57.3 mm (incomplete), width 34.5 mm.
   Locality: Playa Fracasso, Valdes Peninsula, Chubut Province, Argentina.
6. PAGODULA aff. P. CARDUELIS (Watson, 1883) 87
   MPEF-PI-125 (hypotype); height 22 mm (incomplete), width 16.7 mm (incomplete).
   Locality: Puerto Piramide, Valdes Peninsula, Chubut Province, Argentina.
7. STRAMONITA HOMOGENEUS, n. sp. 87
   MPEF-PI-026 (holotype); height 45.7 mm, width 29 mm.
   Locality: Punta Pardela, Valdes Peninsula, Chubut Province, Argentina.

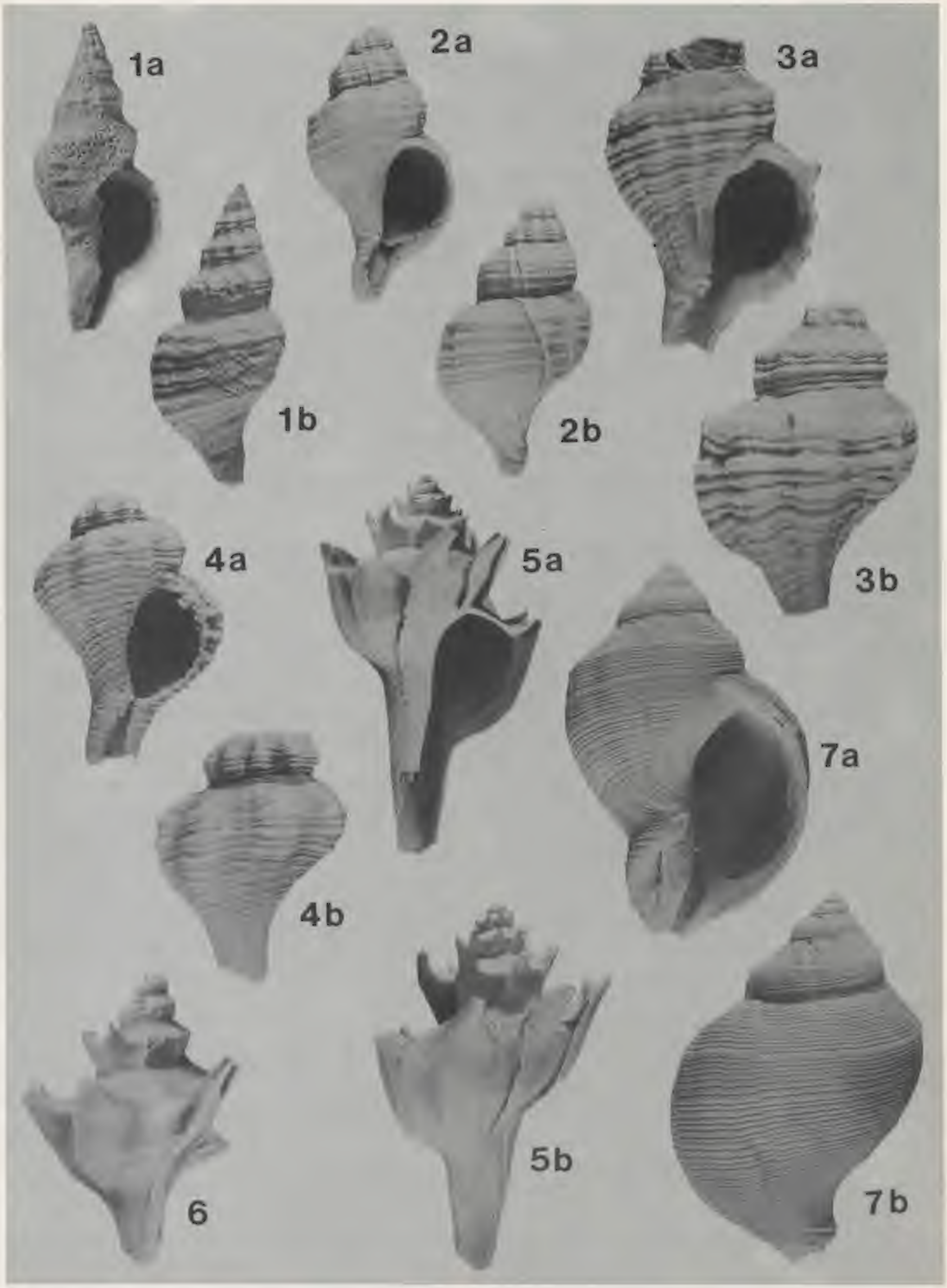

PLATE 5

dentata (Conrad, 1843) has a lip with six denticles, a sigmoidal columellar lip, and axial and spiral ornamentation. *Ilyanassa wilmingtonensis* Gardner, 1948, has a more elongate form, a shallow straight siphonal canal, slightly oblique toward the right with axial and spiral ornamentation. *Ilyanassa isogramma* Dall, 1892, has one inconspicuous columellar plication and a poorly differentiated anterior fasciole. *Ilyanassa obsoleta* (Say, 1822) has one heavy columellar plication, with axial and spiral ornamentation. *Ilyanassa granifera* (Conrad, 1868) has cancellate ornamentation. *Ilyanassa schizopyga* Dall, 1892, is subumbilicate, with a straight anterior siphonal canal and cancellate ornamentation. *Iyanassa johnsoni* (Dall, 1892) has the columellar callus exceedingly developed and axial and spiral ornamentation. *Ilyanassa scalaspira* (Conrad, 1868) differs by its inconspicuous columellar plication and its ornamentation consisting of heavy spaced axial cords and fine spiral striae. *Ilyanassa harpuloides* (Conrad, 1844) has the fasciole poorly developed, shallow siphonal canal and cancellate ornamentation. This is the first record of the genus *Ilyanassa* from the Entrerriense Formation of South America.

Family VOLUTIDAE
Subfamily ZIDONINAE
Genus ADELOMELON Dall, 1906
Subgenus ADELOMELON s.s.
ADELOMELON (ADELOMELON) BECKII
(Broderip, 1836)
Plate 6, figure 2

Description: Shell juvenile, very small, 4 1/2 whorls, with two nepionic whorls; last whorl very elongate and narrow, with deep suture, shoulder marked, very wide, edged with conspicuous tubercules. Lip joined to body-whorl very low, forming an angulation as a consequence of projection of tubercules, then describing a gentle curve, closing in at top of siphonal canal. Columella with heavy callus and two columellar plications, the anterior stronger than the posterior. Shell practically smooth, with only fine growth lines and some inconspicuous, widely spaced spiral striae.

Hypotype: MPEF-PI-259; height 30.3 mm, width 13 mm.

Locality: Puerto Piramide, Valdes Peninsula, Chubut Province, Argentina.

Discussion: We attribute this juvenile example to the species *A. (A.) beckii* because of its general aspect, its protoconch, its very marked shoulder, bordered with tubercules, and its two columellar plications, typical of the species. This is the first record of this species from the Entrerriense Formation of South America.

ADELOMELON (ADELOMELON) FERUSSACII
(Donovan, 1824)
Plate 6, figure 6

Description: Shell of medium size, five convex whorls, two forming protoconch; last whorl inflated, 5 1/2 times height of spire, without tubercules; spire short and pointed. Lip convex, with anal canal inconspicuous, but marked. Aperture wide, with maximum amplitude in anterior third, siphonal canal broken. Columella strongly convex posteriorly, then continuing almost straight, with two heavy plications. Columellar callus very heavy, margined by a glassy surface; fasciole oblique, with marked margin and numerous very imbricate plications. Ornamented with heavy axial cords caused by a great development of growth lines, with fine intermediate cords.

Hypotype: MPEF-PI-243; height 63.2 mm, width 37 mm.

Locality: Puerto Piramide, Valdes Peninsula, Chubut Province, Argentina.

Discussion: The figured specimen presents conchological characters similar to *A. ferussacii*, differing only by the presence of two columellar plications, but in the figure given by Clench and Turner (1964, pl. 98) it is possible to see the presence of only two columellar plications; therefore, this is the first record of this species from the Entrerriense Formation of South America.

Subgenus PACHYCYMBIOLA
Ihering, 1907
ADELOMELON (PACHYCYMBIOLA) aff. A.(P.)
BRASILIANA (Lamarck, 1811)
Plate 6, figure 3

Description: We have only part of the last whorl and posterior edge of the lip. Body-whorl with conspicuous tubercules, which continue forward in the form of fine cords. Posterior labral margin very angulate. Columella convex its entire length; heavy columellar callus and two plications, the anterior much heavier than the posterior.

Hypotype: MPEF-PI-244; measurement impractical.

Locality: Puerto Piramide, Valdes Peninsula, Chubut Province, Argentina.

Discussion: We assign this specimen with some doubt to *A.(P.) brasiliana* on the basis of the heavy posterior labral angulation, the wide callus, and the presence of two unequal columellar plications. This is the first record of the subgenus in the Enterrriense Formation of South America.

Subfamily ODONTOCYMBIOLINAE
Genus ODONTOCYMBIOLA Clench and Turner, 1964

ODONTOCYMBIOLA PARDELENSIS, n. sp.
Plate 6, figure 4

Description: Shell of medium size, only last whorl preserved, that relatively narrow, with a row of tubercules at shoulder. Aperture wide, lip attached to body-whorl at a sharp angle, gradually opening so that aperture is wider in the anterior third. Siphonal canal short but wide. Columella convex posteriorly, practically straight and oblique anteriorly, with two very heavy plications, the anterior more conspicuous. Columellar callus very developed. Ornamented with tubercules prolonged axially by heavy plications. Fasciole oblique, subparallel to columella, not very high, with heavy curved plications.

Holotype: MPEF-PI-245; height incomplete, width 59 mm.

Type locality: Punta Pardela, Valdes Peninsula, Chubut Province, Argentina.

Derivatio nominis: Named for the type locality.

Discussion: Odontocymbiola pardelensis, n. sp., differs from *O americana* (Reeve, 1856) by its outline, which is wider at the shoulder level, appearing less cylindrical, by having only two columellar plications, a better developed callus, a wider siphonal canal, and less conspicuous tubercules. It differs from the varieties of *O. americana*, such as *O. cleryana* Petit, 1856, which has three columellar plications. *Odontocymbiola magellanica* (Gmelin, 1791) differs by generally lacking tubercules, having a much wider last whorl, and a columella with two to five small plications. *Odontocymbiola subnodosa* (Leach) (in Clench and Turner, 1964, p. 155, pls. 95, 96), has one heavy posterior or labral angulation, from three to four columellar plications, but we believe that we can consider our species a good ancestor. This is the first record of the genus *Odontocymbiola* in the Entrerriense Formation of South America.

Family OLIVIDAE
Subfamily OLIVINAE
Genus OLIVANCILLARIA d'Orbigny, 1840

OLIVANCILLARIA PRISCA Ihering, 1907
Plate 6, figure 7

Description: Shell of medium size, oliviform, spire low, conical, apex pointed; suture channeled in final part of last whorl; body-whorl occupying 87% of total height. Aperture subtriangular, anteriorly very wide. Columella with three very heavy oblique plications, fasciole very large, reaching almost to middle of length of aperture. Columellar callus conspicuous, extending to canalicular suture, without covering spire. Ornamented with undulating growth lines.

Hypotype: MPEF-PI-247; height 15 mm, width 6 mm.

Locality: Puerto Piramide, Valdes Peninsula, Chubut Province, Argentina.

Discussion: We consider that this example presents the characters described by Ihering (1907) for *O. prisca*, from the uppermost Entrerriense of Paraná. Figueiras and Broggi (1971-73) mention the species from the Camacho Formation of Uruguay on the basis of internal and external molds with shell remains. Philippi (1893) described, on the basis of a indeterminable mold, *Oliva platensis*; therefore, Ihering decided to denominate the Paraná species as *O. prisca.*

OLIVANCILLARIA FRACASSOENSIS, n. sp.
Plate 6, figure 5

Description: Shell of medium size, heavy. Spire broken; suture canaliculated at least on last whorl; aperture very large, rhomboidal, lip forming a sharp angle with body-whorl and a small posterior siphonal pseudocanal, greatest diameter of aperture in anterior third, then notably narrowing and forming short and narrow anterior siphonal canal. Columella curved, with two conspicuous plications at beginning of anterior third. Columellar callus well developed, not extending to cover spire. Basal fasciole relatively small in proportion; with strong

cords that are a continuation of conspicuous axial cords ornamenting shell.

Holotype: MPEF-PI-248; height incomplete, width 36 mm.

Type locality: Playa Fracasso, Valdes Peninsula, Chubut Province, Argentina.

Derivatio nominis: Named for the type locality.

Discussion: Olivancillaria fracassoensis, n. sp., differs from *O. auricularia* (Lamarck, 1810) by its more elongated form, an aperture posteriorly narrow, with its maximum diameter in the anterior third; its longer and narrower siphonal canal; its columellar plications located more posteriorly, and its small fasciole with heavy cords as ornamentation. In *O. auricularia* the fasciole is smooth, occupying more than 1/3 of the surface of the shell, and is delimited by a fine groove. *Olivancillaria carcellesi* Klappenbach, 1965, has only one basal plication and seven small columellar plications, a deeper anal canal, the width the aperture is greatest anteriorly, and the siphonal canal is shorter and wider. It differs from *O. teaguei* Klappenbach, 1964, which has a height of only approximately 25 mm, a columellar callus slightly developed, a long constricted aperture, ten oblique plications and four longitudinal to the columellar axis. *Olivancillaria urceus* (Röding, 1798) (= *O. brasiliana* Lamarck, 1810) has

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MPEF-PI-242 (hypotype); measurement impractical.
Locality: Puerto Piramide, Valdes Peninsula, Chubut Province, Argentina.
2. ADELOMELON (ADELOMELON) BECKII (Broderip, 1836) 90
MPEF-PI-259 (hypotype); height 30.3 mm, width 13 mm.
Locality: Puerto Piramide, Valdes Peninsula, Chubut Province, Argentina.
3. ADELOMELON (PACHYCYMBIOLA) aff. A.(P.) BRASILIANA (Lamarck, 1811) ...90
MPEF-PI-244 (hypotype); measurement impractical.
Locality: Puerto Piramide, Valdes Peninsula, Chubut Province, Argentina.
4. ODONTOCYMBIOLA PARDELENSIS, n. sp. 91
MPEF-PI-245 (holotype); height incomplete, width 59 mm.
Locality: Punta Pardela, Valdes Peninsula, Chubut Province, Argentina.
5. OLIVANCILLARIA FRACASSOENSIS, n. sp. 91
MPEF-PI-248 (holotype); height incomplete, width 36 mm.
Locality: Playa Fracasso, Valdes Peninsula, Chubut Province, Argentina.
6. ADELOMELON (ADELOMELON) FERUSSACII (Donovan, 1824) 90
MPEF-PI-243 (hypotype); height 63.2 mm, width 37 mm.
Locality: Puerto Piramide, Valdes Peninsula, Chubut Province, Argentina.
7. OLIVANCILLARIA PRISCA Ihering, 1907 91
MPEF-PI-247 (hypotype); height 15 mm, width 6 mm.
Locality: Puerto Piramide, Valdes Peninsula, Chubut Province, Argentina.
8. OLIVELLA aff. O. PLATA (Ihering, 1909) 94
MPEF-PI-251 (hypotype); height 6 mm, width 3 mm.
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9. OLIVANCILLARIA aff. O. URETAI Klappenbach, 1965 94
MPEF-PI-249 (hypotype); height 17.5 mm, width 7.2 mm.
Locality: Puerto Piramide, Valdes Peninsula, Chubut Province, Argentina.
10. OLIVELLA aff. O. PUELCHA (Duclos, 1840) 95
MPEF-PI-250 (hypotype); height 8.5 mm, width 4 mm.
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11. OLIVELLA FRACASSOENSIS, n. sp. 94
MPEF-PI-252 (holotype); height 9 mm, width 3.2 mm.
Locality: Playa Fracasso, Valdes Peninsula, Chubut Province, Argentina.
12. PRUNUM sp. 95
MPEF-PI-253 (hypotype); height 22 mm, width 9 mm.
Locality: Puerto Piramide, Valdes Peninsula, Chubut Province, Argentina.

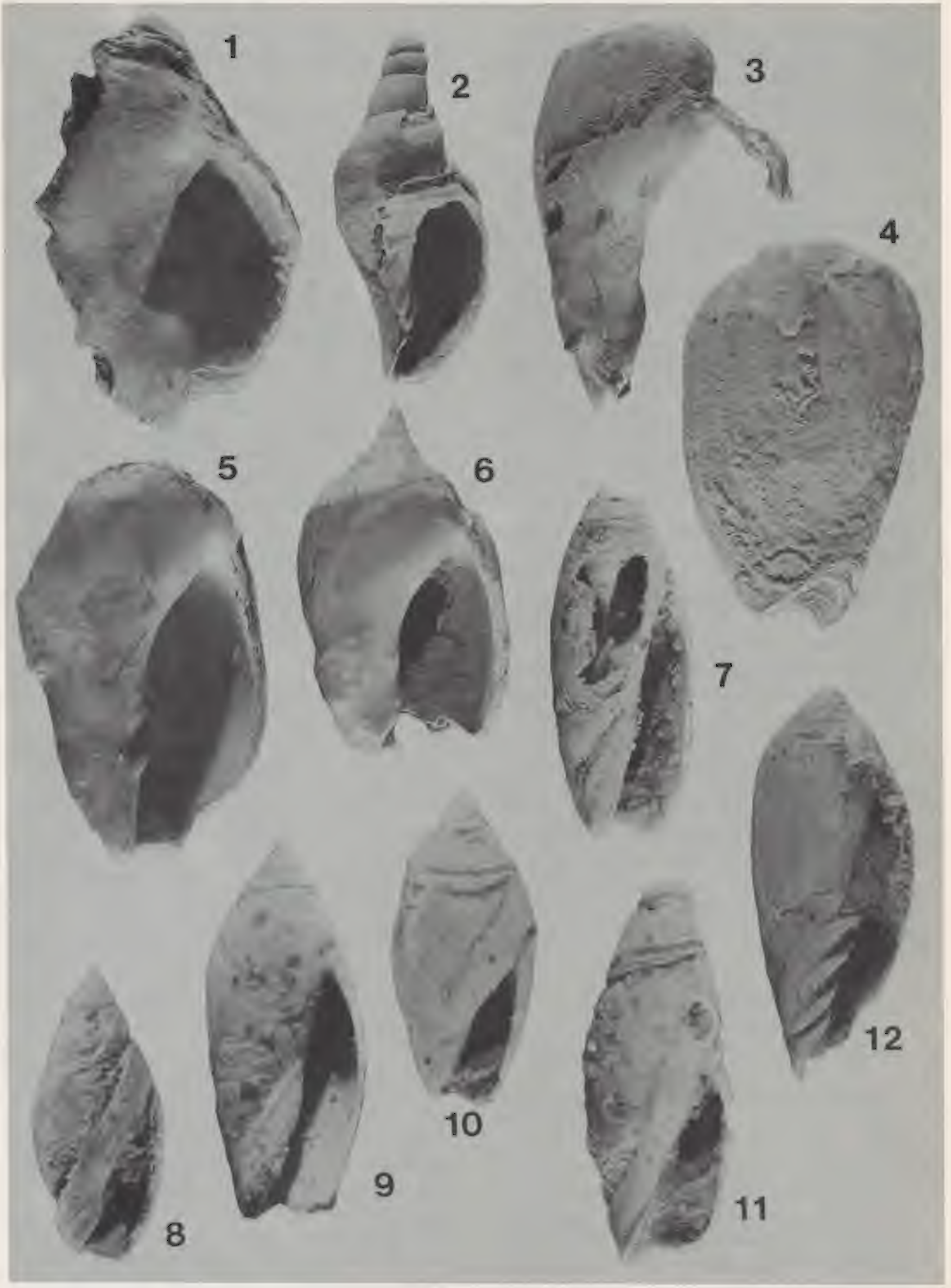

PLATE 6

the last whorl conical, with its greatest diameter posteriorly, a more reduced callus, only one basal plication and small columellar plications, a straight lip, a fasciole occupying 1/3 of the surface of the shell, and a short and wide siphonal canal.

OLIVANCILLARIA aff. O. URETAI
Klappenbach, 1965
Plate 6, figure 9

Description: Shell oliviform, spire low, conical, apex pointed. Suture channeled on final part of last whorl. Callus weak, but extending in an inconspicuous form to sutural channel, without covering spire. Columella almost straight with five to six oblique plications, separated by a groove of the basal plication. Fasciolar band inconspicuous. Aperture occupying four-fifths of total length. Ornamented with undulating growth lines.

Hypotype: MPEF-PI-249; height 17.5 mm, width 7.2 mm.

Locality: Puerto Piramide, Valdes Peninsula, Chubut Province, Argentina.

Discussion: We associate this example with the species *O. uretai,* because of the presence of five to six fine columellar plications, differing in their configuration, being thinner, and presenting an aperture less wide than the living form, but we consider it a valid ancestor to the latter. This is the first record of this species from the Entrerriense Formation of South America. Previously there has been noted from this formation *O. prisca* and *O. urceus* (Röding, 1798), cited as *O. brasiliana*, by Nieves de Medina (1962) from the well at Chuy (Uruguay), at 124 meters depth.

Subfamily OLIVELLINAE
Genus OLIVELLA Swainson, 1831
OLIVELLA aff. O. PUELCHA (Duclos, 1840)
Plate 6, figure 10

Description: Shell very small, conical, elongated, extended, spire sharp; whorls high and narrow. Aperture extended posteriorly, expanding in advance. Sutural channel deep. Columella with only one anterior plication, separated by a groove of the basal plication. Well-developed callus reaching suture, without covering spire. Ornamented with growth lines. Fasciole well marked.

Hypotype: MPEF-PI-250; height 8.5 mm, width 4 mm.

Locality: Puerto Piramide, Valdes Peninsula, Chubut Province, Argentina.

Discussion: We relate this specimen to *O. puelcha* basically by the presence of a single columellar plication. Figueiras and Broggi (1971-73) mention this species from the Barranca de San Pedro, Colonia (Camacho Formation); consequently this is the first record from the Entrerriense Formation of Argentina. From the Middle Miocene of Brasil, Closs (1970), cited *Olivella (Olivina) bullula* (Reeve, 1850) and *Olivella (Toroliva) goliath* Olsson, 1922.

OLIVELLA aff. O. PLATA (Ihering, 1909)
Plate 6, figure 8

Description: Shell small, slender, spire thin, whorls high, suture deep; last whorl narrow; callus slightly marked, extending past aperture, but not reaching to suture. Lip weakly curved. Columella barely concave, with one wide basal plication and a second very marked plication above dorsum of shell, separated from the first by a conspicuous groove.

Hypotype: MPEF-PI-251; height 6 mm, width 3 mm.

Locality: Puerto Piramide, Valdes Peninsula, Chubut Province, Argentina.

Discussion: This species is living from the coast of the Province of Buenos Aires to the Golfo Nuevo. It has been recorded from the Pampeano of Puerto Militar, Ihering (1907) citing it as *Olivancillaria auricularia plata*, and from the Interensenadense of Punta Piedras. The fossil examples differ from the living ones only by the greater posterior expansion of the callus, which reaches to the suture. This is the first report of this species from the Entrerriense Formation of South America.

OLIVELLA FRACASSOENSIS, n. sp.
Plate 6, figure 11

Description: Shell small, elongated and slender, spire very high and pointed; sutures deep; whorls of spire convex. Body-whorl corresponding to 87% of total height; aperture enlarging very little anteriorly, its length representing 47% of total height. Callus reaching sutural channel, without covering spire. Only one columellar plication, separated from basal plication by a groove. Columella rather concave due

to presence of conspicuous indentation beginning at siphonal canal. Fasciole inconspicuous and smooth.

Holotype: MPEF-PI-252; height 9 mm, width 3.2 mm. Body-whorl: length 7.8 mm. Aperture: length 4.2 mm.

Type locality: Playa Fracasso, Valdes Peninsula, Chubut Province, Argentina.

Derivatio nominis: Named for the type locality.

Discussion: Olivella fracassoensis, n. sp., differs from *O. puelcha*, in having only one columellar plication; it is much higher and narrower, with less expansion of the aperture anteriorly, spire much higher, and columellar indentation. It differs from *O. plata* by having one very wide basal plication and a second plication over the dorsum of the shell; it has a lower spire and narrower body-whorl. *Olivella carolinae* Gardner, 1948, has an ovoid-conical form, being of much greater size (16.2 mm in height), the aperture is wider anteriorly, the spire proportionally lower, the body-whorl much wider and lacking the columellar indentation.

Family MARGINELLIDAE
Genus PRUNUM Herrmansen, 1852
PRUNUM sp.
Plate 6, figure 12

Description: Shell medium-sized, elongate, relatively oviform; spire low, aperture apparently narrow, outer lip destroyed. Columella straight, with four heavy plications; columellar callus appearing to reach only to middle of aperture; siphonal canal destroyed.

Hypotype: MPEF-PI-253; height 22 mm, width 9 mm.

Locality: Puerto Piramide, Valdes Peninsula, Chubut Province, Argentina.

Discussion: The example described is unique, being found almost destroyed. We tentativaly place it in the genus *Prunum* because of the apparently low spire, the lip begining below the spire, with a sharp angle, and with four columellar plications. Castellanos (1967) lists *Marginella prunum* (Gmelin, 1791) from the Antilles, Brasil, Uruguay, and Argentina, as far south as Golfo San Matias. Figueiras and Broggi (1971-1973) cited *Prunum pruniformis* (Ihering, 1907) from the Barranca de San Pedro, Uruguay (Camacho Formation); while from the marine Miocene of southern Brasil they cited *Prunum prunum* (Gmelin, 1791). This is the first record of the genus *Prunum* in the Entrerriense Formation of Argentina.

Subclass HETEROBRANCHIA
Order ALLOGASTROPODA
Superfamily PYRAMIDELLOIDEA
Family PYRAMIDELLIDAE
Subfamily TURBONILLINAE
Genus TURBONILLA Risso, 1826
TURBONILLA URUGUAYENSIS Pilsbry, 1897
Plate 7, figure 1

Description: Shell turriform, slender, strong. Ten almost straight whorls, with conspicuous sutures; first whorls smooth, later whorls with fine oblique ribs, on last whorls these becoming heavier, tabulate, and vertical. Aperture subquadrate, with columella practicaly vertical, simple and rather tilted toward base. Base only with growth lines.

Hypotype: MPEF-PI-254; height 7.7 mm, width 2.1 mm.

Locality: Puerto Piramide, Valdes Peninsula, Chubut Province, Argentina.

Discussion: The fossil specimen presents the conchological characters of the living species. Figueiras and Broggi (1971-73) list *Turbonilla* sp. from the Camacho Formation of Uruguay, undoubtedly assignable to the subgenus *Pyrgiscus*. From the marine Miocene of southern Brasil is listed for the genus *Pyramidella* Lamarck, 1799, *P. candida* Mörch, 1875, and for the genus *Turbonilla* Risso, 1826, *T. (Pyrgiscus) interrupta* Totten, 1835. Brown and Pilsbry (1913) proposed as forms representing the genus *Turbonilla* from the Gatun Formation (Late Miocene), *T. bartschiana* and *T. gatunensis*. This is the first record of the genus *Turbonilla* in the Entrerriense Formation of Argentina.

Subgenus PYRGISCUS Philippi, 1841
TURBONILLA (PYRGISCUS) sp.
Plate 7, figure 2

Description: Shell very small, thin, with 9 1/2 convex whorls; sutures conspicuous; first whorls smooth, the following whorls with fine axial ribs, on last whorls these becoming somewhat heavier, with addition of heavy spiral cords. Base with strong spiral striations. Aperture subquadrate; columella almost straight.

Hypotype: MPEF-PI-255; height 5 mm, width 1.1 mm.

Locality: Puerto Piramide, Valdes Peninsula, Chubut Province, Argentina.

Discussion: This unique example is almost complete, but in bad condition. It is characterized by the heavy spiral ornamentation on the last whorls; therefore, it is assigned with doubt to the subgenus *Pyrgiscus*. From the marine Miocene of Brasil *T.(P.) interrupta* Totten, 1835, has been recorded; consequently, this is the first record from the Entrerriense Formation of Argentina.

Subclass OPISTOBRANCHIA
Order CEPHALASPIDEA
Superfamily PHILINOIDEA?
Family SCAPHANDRIDAE
Genus ACTEOCINA Gray, 1847

ACTEOCINA PIRAMIDESIA, n. sp.
Plate 7, figure 3

Description: Shell very small, slender, subcylindrical. Spire low, visible only in apertural view, dorsally only the protoconch visible, lacking in this example. Posterior margin of lip very elevated, reaching same height as spire, lateral margin parallel to body-whorl, with aperture very narrow; anteriorly lip opening widely. Base of columella broken; therefore, plications unknown. Exteriorly smooth under microscope (X 40).

Holotype: MPEF-PI-256; height 6 mm, width 3 mm.

Type locality: Puerto Piramide, Valdes Peninsula, Chubut Province, Argentina.

Derivatio nominis: Named for the type locality.

Discussion: Acteocina piramidesia, n. sp., differs from *A. bullata* (Kiener, 1834), living in the West Indies, which has the lip straight, without anterior expansion, the aperture wider and spiral striations as ornamentation. *Acteocina elachista* Woodring, 1970, has a higher spire, the aperture beginning below the shoulder of the body-whorl is much wider and without anterior expansion. *Acteocina rusa* Gardner, 1937, has a higher spire, the aperture begins below the shoulder of the whorl; it is much wider, lacks an anterior expansion, and is ornamented with axial striations. *Acteocina candei* (d'Orbigny, 1842), living from the Antilles to Puerto Quequen (Prov. Bs. Aires), has the spire more elevated, the aperture beginning below the shoulder of the body-whorl is wider and lacks the anterior expansion. According to the author there are fine spiral striations. This is the first record for the Entrerriense Formation of South America.

Family RETUSIDAE
Genus VOLVULELLA Newton, 1891

VOLVULELLA aff. V. PHOINICOIDES
(Gardner, 1937)
Plate 7, figure 4

Description: Shell of small size, cylindrical, very thin; height three times width. Apical spine short, twisted, leaving a depresion between spine and shell. Outer lip thin, anteriorly expanded forming a flange. Strong columellar callus. Microscopically (X 40) no ornamentation seen.

Hypotype: MPEF-PI-257; height 3 mm, width 1.1 mm.

Locality: Puerto Piramide, Valdes Peninsula, Chubut Province, Argentina.

Discussion: This specimen is the only example obtained to date. From the conchological characters it is near *V. phoinicoides*, especially in its apical characters and its measurements. It differs by the structure of the anterior end, with a conspicuous columellar callus. This is the first record of the genus *Volvulella* from the Entrerriense Formation of South America.

Subclass PULMONATA
Order STYLOMMATOPHORA
Suborder ELASMOGNATHA
Superfamily SUCCINEOIDEA
Family SUCCINEIDAE
Subfamily SUCCINEINAE
Genus SUCCINEA Draparnaud, 1801

SUCCINEA MERIDIONALIS d'Orbigny, 1846
Plate 7, figure 5

Description: Shell diminutive, thin and fragile, translucent, imperforate; consisting of three convex whorls, the last representing more than two-thirds of total height; spire short with linear sutures, deep and inclined. Aperture elongate-oval, wider anteriorly, holoperistomate. Exteriorly smooth, with only growth lines.

Hypotype: MPEF-PI-258; height 7 mm, width 6 mm. Body-whorl: length 6 mm.

Locality: Puerto Piramide, Valdes Peninsula,

Chubut Province, Argentina.

Discussion: The presence of a pulmonate gastropod is not new to the Tertiary of Patagonia. Ihering (1907) mentioned for the Entrerriense of Paraná, as well as for the gray sands of the Rionegrense, the genera *Strophocheilus, Chilina, Ampullaria, Diplodon* and *Corbiculella*; also in that work are described species of the genus *Littorina* from waters typically brackish. But this is the first mention of the genus *Succinea* from the Entrerriense Formation of South America. We have no doubts with respect to the stratigraphic position of this example, having been obtained in depth and sieved from the sediments.

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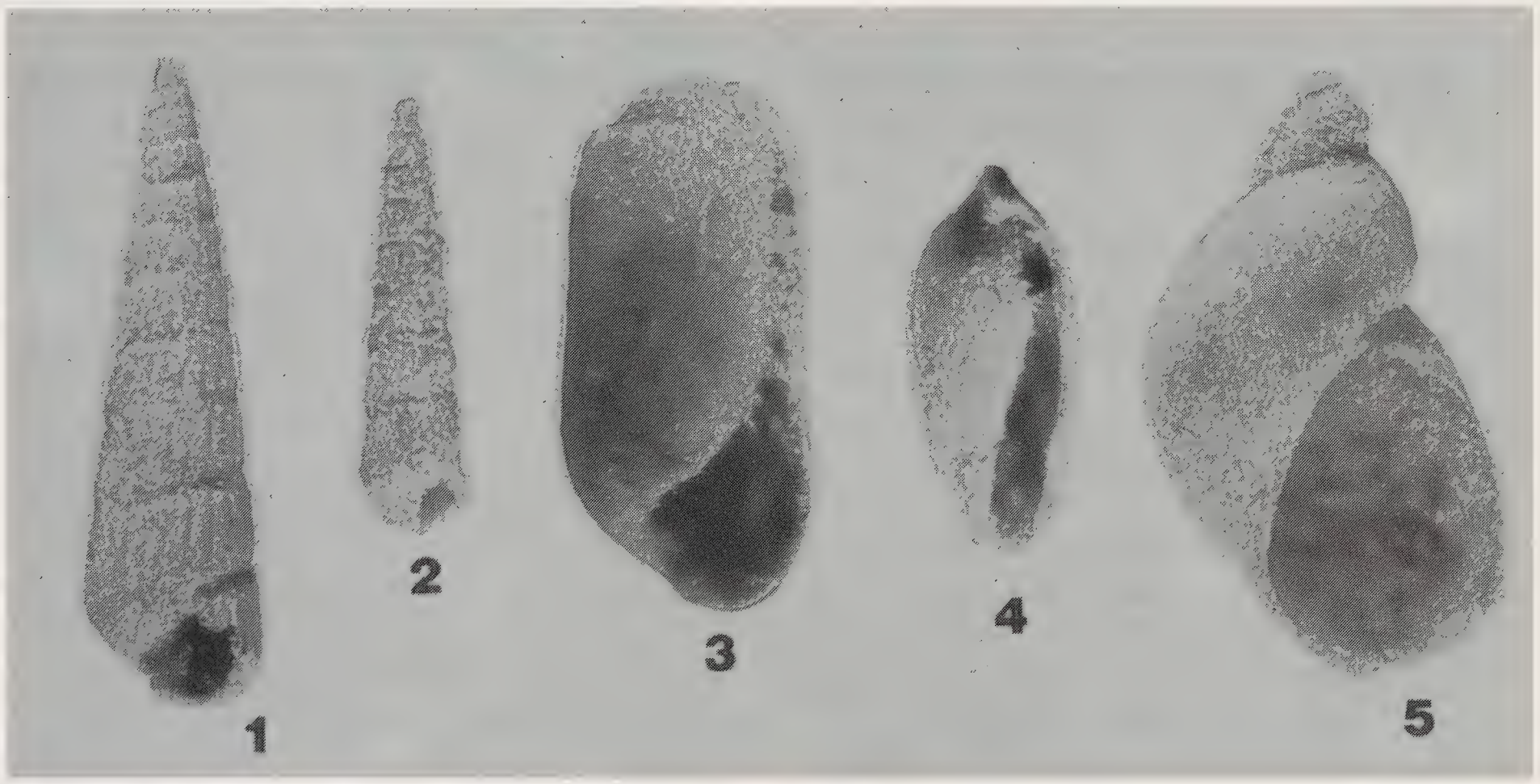

PLATE 7

Figures Page

1. TURBONILLA URUGUAYENSIS Pilsbry, 1897 95
   MPEF-PI-254 (hypotype); height 7.7 mm, width 2.1 mm.
   Locality: Puerto Piramide, Valdes Peninsula, Chubut Province, Argentina.
2. TURBONILLA (PYRGISCUS) sp. 95
   MPEF-PI-255 (hypotype); height 5 mm, width 1.1 mm.
   Locality: Puerto Piramide, Valdes Peninsula, Chubut Province, Argentina.
3. ACTEOCINA PIRAMIDESIA, n. sp. 96
   MPEF-PI-256 (holotype); height 6 mm, width 3 mm.
   Locality: Puerto Piramide, Valdes Peninsula, Chubut Province, Argentina.
4. VOLVULELLA aff. V. PHOINICOIDES (Gardner, 1937) 96
   MPEF-PI-257 (hypotype); height 3 mm, width 1.1 mm.
   Locality: Puerto Piramide, Valdes Peninsula, Chubut Province, Argentina.
5. SUCCINEA MERIDIONALIS d'Orbigny 1846 96
   MPEF-PI-258 (hypotype); height 7 mm, width 6 mm.
   Locality: Puerto Piramide, Valdes Peninsula, Chubut Province, Argentina.

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OCCURRENCE OF THE REGULAR URCHIN *EUCIDARIS TRIBULOIDES* FROM THE TAMIAMI FORMATION (PLIOCENE) OF FLORIDA

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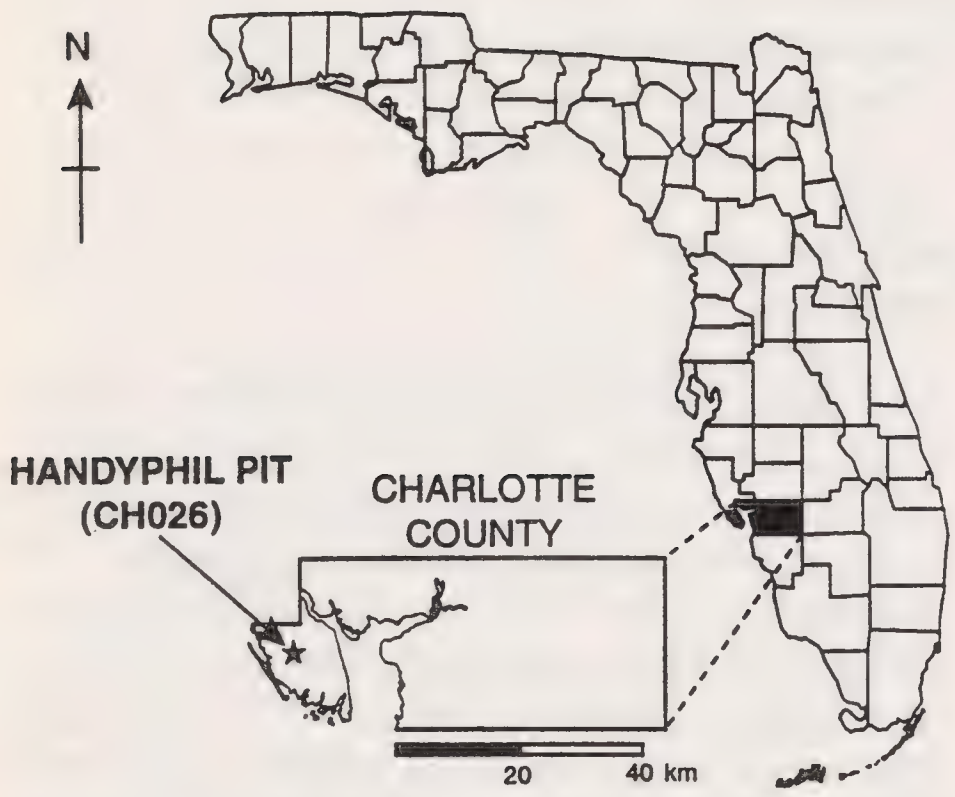
The echinoids of the Pliocene Tamiami Formation of Florida are typically abundant, well-preserved, and reasonably well-known. In a 1963 monograph, Kier listed nine species of echinoids from the Tamiami Formation. These were *Arbacia crenulata* Kier, 1963, *Lytechinus variegatus plurituberculatus* Kier, 1963, *Clypeaster crassus* Kier, 1963, *C. sunnilandensis* Kier, 1963, *Encope tamiamiensis* Mansfield, 1932, *E. michelini imperforata* Kier, 1963, *Mellita aclinensis* Kier, 1963, *Rhyncholampas evergladensis* (Mansfield, 1932), and *Echinocardium gothicum* (Ravenel, 1848). Phelan (1972) eliminated previous confusion between *E. michelini* L. Agassiz, 1841, and *E. aberrans* Martens, 1867, and re-identified Kier's *E. michelini imperforata* as *E. aberrans*. Kier (1992) agreed with Phelan's specific assessment but still considered his earlier (1963) subspecific designation to be valid. Since Kier (1963), no new additions to the echinoid fauna of the Tamiami Formation have been reported, until now.

Between 1989 and 1996, fossil collections were made by the Invertebrate Paleontology staff and volunteers of the Florida Museum of Natural History (FLMNH) at University of Florida (UF) locality CH026 (also known as the HandyPhil Pit) in western Charlotte County, Florida (text-figure 1). These collections yielded hundreds of isolated regular urchin test plates and radioles and three partial, but flattened, regular urchin tests (UF 39528, UF 60203, and UF 72022). Recent analysis of these urchin remains indicates that they belong to *Eucidaris tribuloides* (Lamarck, 1816), a genus and species not previously recorded from the Florida fossil record. Other common taxa collected at this locality included the brachiopod, *Glottidia inexpectans* Olsson, 1914; the gastropods, *Dicathais handgenae* Portell and Vokes, 1992, and *Ecphora quadricostata* (Say, 1824); the barnacle, *Tamiosoma advena* Zullo, 1992; and the echinoids, *Echinocardium gothicum* (Ravenel, 1848) and *Encope tamiamiensis* Mansfield, 1932. Numerous pectens and oysters were also collected. All specimens from UF locality CH026 were collected in a gray, medium- to fine-grained quartz sand with a modest amount of heavy mineral content. No aragonitic-shelled taxa were preserved, only calcitic-shelled taxa typically associated with the Tamiami Formation were present (see taxa above). At UF locality CH026, the Tamiami Formation is overlain by a 2 meter thick shell bed attributable to the Fort Thompson Formation.

Other fossil occurrences of *E. tribuloides* are known from outside Florida. Donovan and Embden (1996) summarized the Jamaican occurrences, including specimens from the Plio-Pleistocene August Town Formation, early Pleistocene Manchioneal Formation and Old Pera Beds, and late Pleistocene Port Morant and Falmouth formations. Elsewhere, Lewis and Donovan (1991) reported radioles from the Pliocene and late Pleistocene of Tobago. Cutress (1980) confirmed several published reports from the Plio-Pleistocene Playa Grande Formation, and Pleistocene Abisinia, Cerro Gato, and Tortuga formations of Venezuela. Cutress also discounted reports by Jackson (1922) and Sánchez Roig (1949) of *E. tribuloides* from the Miocene (?) of Cuba.

Extant *E. tribuloides* occurs from Cape Hatteras, North Carolina, east to Bermuda, throughout the Caribbean, the Gulf of Mexico, and south to Rio de Janeiro, Brazil (Serafy, 1979). Its known depth range has been recorded between 0 and 800 meters. However, it is most commonly found at depths of less than 50 meters (Serafy, 1979). *Eucidaris tribuloides* inhabit rocky areas, typically under rocks and in small crevices. They are also known to inhabit seagrass beds (Hendler *et al.*, 1995).



Text Figure 1. Map showing locality of the first reported occurrence of the fossil *Eucidaris tribuloides* (Lamarck, 1816) from Florida.

ACKNOWLEDGMENTS

We are indebted to Phillip Whisler of Gainesville, Florida for his assistance in the field, and particularly, for collecting and donating fossil *E. tribuloides* specimens UF 72022 and UF 60203. Jimmy and Pat Philman, Englewood, Florida, kindly allowed access to their shell pit (UF locality CH026). Burchard Carter, Georgia Southwestern State University and Stephen Donovan, University of the West Indies reviewed earlier drafts of the manuscript and provided helpful comments. This is University of Florida Contribution to Paleontology 486.

SYSTEMATIC PALEONTOLOGY

Class ECHINOIDEA Leske, 1778
Order CIDAROIDA Claus, 1880
Family CIDARIDAE Gray, 1825
Genus EUCIDARIS Döderlein, 1887
EUCIDARIS TRIBULOIDES (Lamarck, 1816)
Plate 1, figures 1a-b, 2, 3

Description: Test typically flattened both adapically and adorally. Primary tubercles noncrenulate, perforate, having a conical boss nearly circular in outline, and grading into scrobicule without a basal terrace. Areoles circular at ambitus, becoming transversely elongate near apical and oral regions. Scrobicular tubercules only modestly larger than surrounding secondary tubercles.

Ambulacra are narrow, slightly sinuous, and widest at ambitus. Poriferous zones in minor, sunken grooves. Pores round to slightly elliptical, separated by a low, interporal partition. Ambulacra approximately one-fourth as wide as interambulacra areas.

Interambulacra plates up to two times wider than tall. Interradial tract about two times wider than adradial tract. Secondary tubercles densely distributed throughout plate surface. Interradial suture simple, non-serrate.

Primary radioles have limited shape variation, but include both cylindrical and truncate forms. Shaft may be slightly inflated in proximal to medial portion. Acetabulum diameter approximately 44-61% of radiole width. Radioles up to 42.9 mm long, and 3.5 to 4.5 mm wide. Milled ring is located 2.0 to 2.7 mm above base, and collar is 1.6 to 2.4 mm long with conical shape widest at milled ring. Neck is narrow and located 3.5 to 4.6 mm above base. Shaft has numerous longitudinal series of low nodules, which may not be visible on more poorly preserved or altered samples. Distal end of radioles marked by low-ribbed crown, with a central prominence.

The three flattened tests (UF 72022, UF 60203, 39528) are incomplete and compacted; therefore, not all diagnostic features are well-preserved. More detailed species descriptions are available in Weisbord (1969), Phelan (1970), Cutress (1980), Donovan (1993), and Hendler *et al.* (1995).

Discussion: Comparison of the fossil specimens from the Tamiami Formation with several modern *E. tribuloides* specimens from the Florida Keys show most morphologic characteristics to be similar among the samples. The Florida fossils also are comparable with *E. tribuloides* described by Donovan (1993) from the Falmouth Formation (Pleistocene) in Jamaica, as well as samples of this species reported by Weisbord (1969) from the Playa Grande Formation of Venezuela (Plio-Pleistocene). Many of Weisbord's Venezuelan samples are now reposited in the Florida Museum of Natural History and, therefore, were available for comparison by the authors.

Cutress (1980) compared samples of fossil and modern *E. tribuloides* collected from sites in the Caribbean and Gulf of

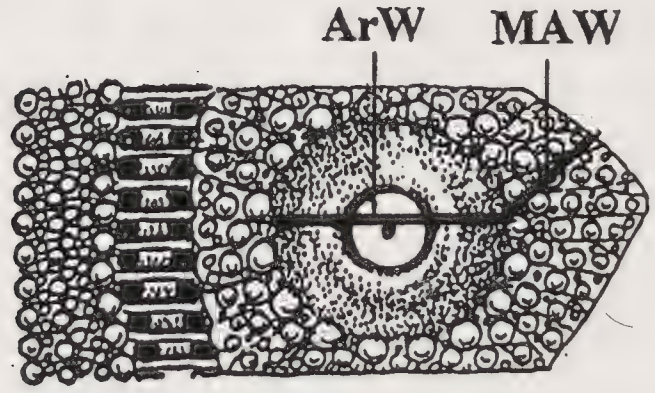
Eucidaris tribuloides Biometrics Summary

I. Modern *Eucidaris tribuloides*

Number of Plates Measured	Mean of Medial Area Width (MAW)	Mean of Areole Width (ArW)	MAW / ArW Ratio Mean
n=15	$\bar{x}$=2.48 mm	$\bar{x}$=6.18 mm	$\bar{x}$=0.40

II. Fossil *Eucidaris tribuloides* (Tamiami Formation, Pliocene)

Number of Plates Measured	Mean of Medial Area Width (MAW)	Mean of Areole Width (ArW)	MAW / ArW Ratio Mean
n=20	$\bar{x}$=4.32 mm	$\bar{x}$=7.32 mm	$\bar{x}$=0.58



Text Figure 2. Summary statistics for single-plate measurements of medial area width (MAW), areole width (ArW), and medial area width / areole width ratio (MAW / ArW). Measurements are in mm, and were obtained from locations indicated on the test plate illustration and discussed in the text. (Illustration modified from Cutress, 1980).

Mexico region with several fossil and/or modern species of *Eucidaris*, including *E. madrugensis* (Sánchez Roig, 1949), *E. thouarsii* (Valenciennes, 1846), and *E. clavata* Mortensen, 1928. Cutress reported several key differences between *E. tribuloides* and each of these species using both qualitative and quantitative (biometric) characteristics, and we have summarized these differences here. *Eucidaris clavata*, a modern species known only from Ascension and St. Helena Islands in the South Atlantic, has fewer interambulacral plates per column, contains more confluent areoles, and lacks fan-shaped septal bundles. Biometric analysis of the two species completed by Pawson (1978) revealed significant differences in the ratio of the median area width (MAW) of the interambulacral plates to the associated areole width (ArW), as well as in the ratio of the apical system diameter (ApD) to the peristome diameter (PerD) for the species. He reported a mean MAW/ArW ratio of 0.51 for *E. clavata* and 0.97 for *E. tribuloides*, while the ApD/PerD mean ratio was 0.77 for *E. clavata* and 1.02 for *E. tribuloides.*

Eucidaris thouarsii, a Recent species from the eastern Pacific Ocean, has wider median areas on interambulacral plates and wider associated areoles. Data accumulated by Chesher (1972) for the ratio of MAW/ArW of *E. tribuloides* shows a ratio range of 0.6-0.8, while on equivalent-sized specimens of *E. thouarsii*, Cútress (1980) calculated the mean ratio to be slightly lower, 0.58, over a range of 0.4-0.78. An additional biometric ratio, areole width (ArW) to the width of a single interambulacral plate (IAmPlW) also supports a separation of the species, with the ArW/IAmPlW mean ratio for *E. thouarsii* equal to 0.68 whereas for *E. tribuloides* the mean ratio is equal to 0.58.

Finally, comparisons with *E. madrugensis* are important, though the characters of this species are somewhat difficult to deci-

pher from the literature. Jackson (1922) and Sánchez Roig (1949) reported cidaroid specimens from the Miocene of Cuba, which Cutress subsequently reassigned to *E. madrugensis*. Sánchez Roig (1949) caused confusion in the process of naming the species, by using both the names *Dorocidaris madrugensis* (in the text) and *Leiocidaris madrugensis* (in the figure caption) for the same series of figures in his plates. Furthermore, Cutress (1980) determined through examination of the figured specimens that not all of the specimens were actually eucidarids, but were Cretaceous phyllacanthid species instead. Cutress determined that *E. madrugensis* is closely related (likely the ancestral form) to *E. tribuloides*, but differs by having whorled radioles in adults, a larger areole width, and having radiole collars that are only half as long as in *E. tribuloides*. In addition, Donovan and Paul (in press) described the presence of low spinules on the primary radioles of *E. madrugensis* whereas primary radioles of *E. tribuloides* do not possess such spinules.

A cautionary note must be made regarding the biometric data gathered and their use in the diagnostic ratios described above. Cutress (1980) pointed out that in most of her measurements of median area width (MAW) and calculations of the MAW/ArW ratios, she used only single-plate measurements. Since most of her work dealt with fossil cidaroids rather than modern specimens, she recognized that imperfect preservation of the fossils often resulted in incomplete skeletal remains to identify and measure. This is in contrast to Pawson (1978) and Mortensen (1928), where they determined the usual, "entire" median area measurements from the pair of associated and articulated interambulacral plates. The difference between these methods will cause a different ratio to result, because only one of the two plates and its width is considered. Since the sum of two single-plate median area widths is not equal to the "entire" median area width determined from two plates, one cannot simply extrapolate data from one set to the other. A second problem in examining the data is distinguishing from which region on the plates a median area width was measured. Each interambulacral plate is pentagonal in outline, but the apex of the pentagon is asymmetrical, so measurements will vary unless specific endpoints are identified for the median area width position. No specific diagrams were provided in Pawson (1978) or Cutress (1980) to illustrate exactly where their measurements are located on the test plates, making replication of equivalent measurements on the Tamiami Formation specimens illustrated in Plate 1 less certain.

Text-figure 2 shows summary data and calculations for MAW, ArW, and MAW/ArW ratios (using single-plate measurements) for a specimen of *E. tribuloides* from the Florida Keys and for several FLMNH samples of the fossil *E. tribuloides* reported herein. In addition, text-figure 2 illustrates the exact location measured on each plate, for each of the biometric variables, to help alleviate any confusion in how our ratios were determined. It is interesting to note that the MAW/ArW mean ratio for the Florida fossils is 0.58 while the modern specimen has a mean ratio of 0.40. The implications of this may be that the fossil material is not from *E. tribuloides*, but rather a new species. Pawson (1978) believed such biometric ratios important enough to justify specific differentiation between *E. clavata* and *E. tribuloides*, so such variation between the modern and fossil samples used in this study may warrant further examination and interpretation if more complete specimens are recovered in the

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PLATE 1

Figures 1-3. *Eucidaris tribuloides* (Lamarck, 1816)

1a-b. UF 72022. a. Oral surface of flattened test showing partially exposed lantern.
b. Aboral surface of flattened test. Both X1.

2. UF 60203. Lateral view of flattened test. X1.

3. UF 80300. Radiole. X2.

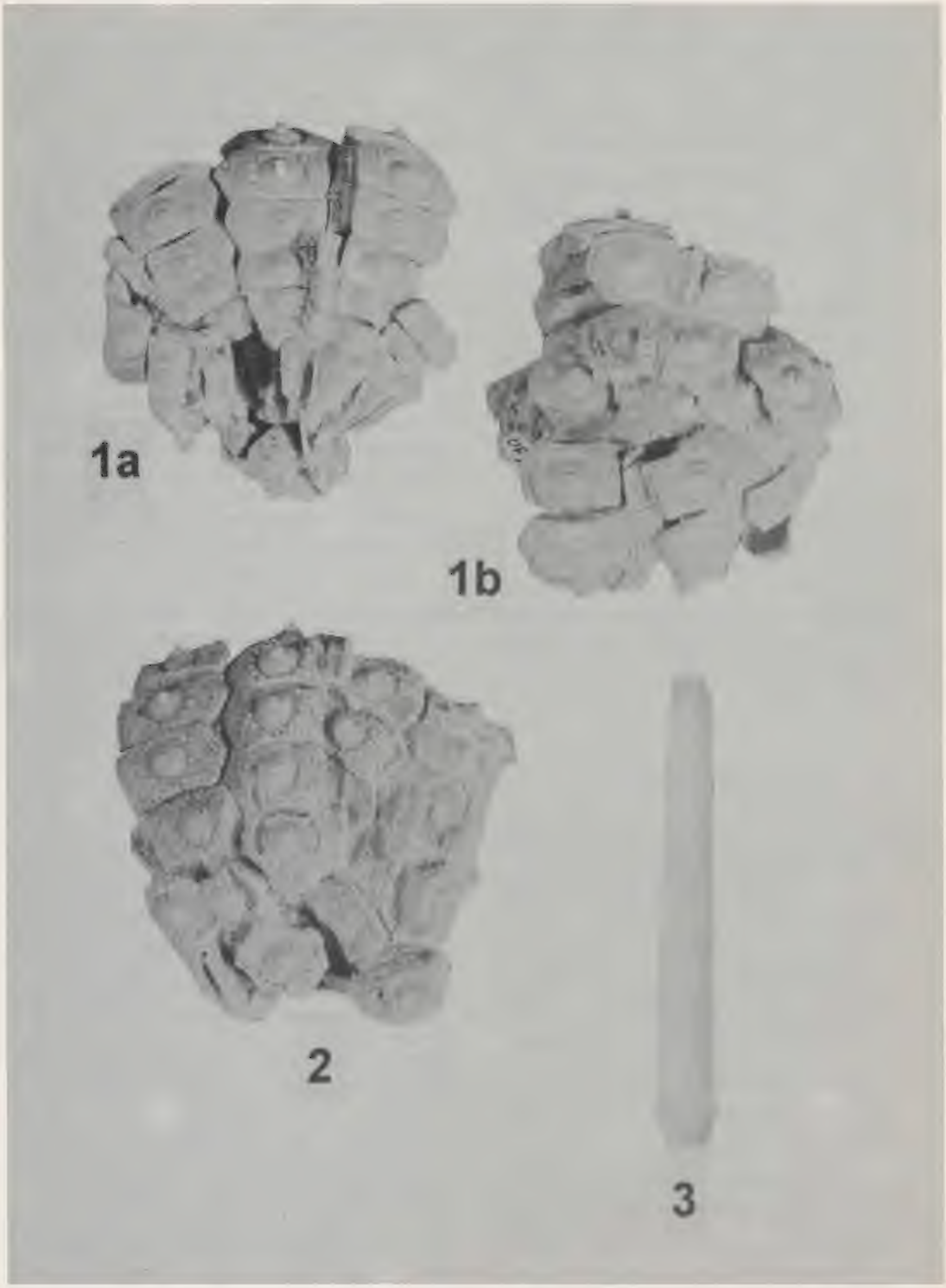

PLATE 1

future. Unfortunately, the fossils currently available are not articulated and have been flattened during fossilization, preventing a more thorough qualitative and quantitative analysis of the specimens with a broader group of biometric features. It appears as though at least two of the three best fossil specimens are near the largest end of the size range reported for *E. tribuloides*. However, without better preserved fossil specimens, it is impossible to justify a new species description. Based on the fossils currently available, we believe the best interpretation is to treat them as *E. tribuloides*. This is the first fossil occurrence of this species from the United States.

LOCALITY DATA

The following is a collecting locality of the Invertebrate Paleontology Division, Florida Museum of Natural History, University of Florida (UF).

CH026 Shell pit approximately 1.2 kilometers east of Grove City, Charlotte County, Florida (NE 1/4, NE 1/4, Sec. 16, T41S, R20E; Englewood Quadrangle, USGS 7.5 minute series, 1987).

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August 27, 1997

NOTES ON THE FAUNA OF THE CHIPOLA FORMATION – XLI
A REEXAMINATION OF *BURSA* (MOLLUSCA: GASTROPODA) FROM THE CHIPOLA FORMATION, WITH THE DESCRIPTION OF A NEW SPECIES

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In 1973 Emily Vokes reviewed the genus *Bursa* in the Alum Bluff Group and identified Chipola Formation specimens collected from Tenmile Creek, Farley Creek, and the Chipola River as *Bursa pelouatensis* (Cossmann and Peyrot, 1923). Although *Bursa pelouatensis* is a European species from the Aquitaine Basin of France, Vokes noted that the Chipola specimens and their French counterpart have similar spiral ornamentation and varices that are not aligned up the spire (1973, p. 97). It was these characteristics that led her to conclude that both the Chipola and Aquitaine Basin specimens belong to the same species.

Recently this investigator was given an opportunity to examine a complete growth series of *Bursa pelouatensis* from the Aquitaine Basin and compare them with Chipola specimens collected along Tenmile Creek and Chipola River. Although both the Chipola and Aquitaine Basin species exhibit the similarities reported by Vokes, it is this investigator's opinion that there are sufficient morphological differences between the two to justify describing the Chipola form as a separate species.

A visual comparison of the two forms of *Bursa* is presented in plate 1, figures 1 and 2. These photographs clearly illustrate that the Chipola shell is broader, squatter and possesses more pronounced nodular and beaded sculpturing on the body whorls than its Aquitaine Basin counterpart. In addition, the Chipola species consistently has a better developed anal channel, the shoulders are straighter, and the neck of the body whorl arches more acutely to left. It is these differences that have led this investigator to recognize the Chipola form as a new species.

Family BURSIDAE Thiele, 1925
Genus BURSA Röding, 1798

Bursa RÖDING, 1798, Museum Boltenianum, p. 128.

Type species: *Murex bufonius* Gemlin, 1791 (by subsequent designation, Jousseaume, 1881, p. 174).

Subgenus BUFONARIELLA Thiele, 1929

Bufonariella THIELE, 1929, Systematischen Weichtierkunde, v. 1, pt. 1, p. 284.

Type species: *Murex scrobilator* Linné, 1758 (by monotypy).

BURSA (BUFONARIELLA) CHIPOLANA Schmelz, n. sp.
Plate 1, figure 1
Plate 2, figures 1, 2

Bursa pelouatensis (Cossmann and Peyrot). VOKES, 1973, Tulane Stud. Geol. Paleont., v. 10, no. 2, p. 97, text-fig. 2 (not of Cossmann and Peyrot).

Description: Protoconch worn in all specimens. Shell bulbous, not flattened dorso-ventrally. Two varices on each body whorl; varices not aligned up spire, strongly offset on body whorl. Postnuclear whorls five; sculptured with seven, strongly noded intervarical tubercles, best developed along edge of shoulder on body whorl. Beaded spiral cords and faint spiral threads traversing nodes and internodal spaces; suture distinct. Shoulder prominent, slightly downward sloping. Aperture oval; outer margin fluted, reflexed anteriorly, bearing nine to eleven lirae along inside edge. Parietal callus strongly wrinkled; posterior canal U-shaped, well-developed, arching backwards; siphonal canal short, slightly reflexed.

Holotype: UF 73199; height 46.0 mm, maximum diameter 29.0 mm.

Type locality: TU 546, Chipola Formation, Tenmile Creek, about 1 3/4 miles west of Chipola River (NE 1/4 Sec. 12, T1N, R10W), Calhoun Co., Florida (=USGS 2212, "one mile west of Bailey's Ferry").

Paratype A: USNM 647108; height 48.3 mm, maximum diameter 30.8 mm; locality TU 547.

Paratype B: UF 73200; height 35.0 mm, maximum diameter 24.2 mm; locality TU 951.

Additional unfigured paratypes: Three specimens from TU 951 (two from the Bell collection and one from the Schmelz collection) and one specimen from TU 546 (Murray collection); Tulane Collection, locality numbers TU 546, 547, 1051, 1098, 1196.

Discussion: In his paper on the family Bursidae, Beu (1980, p. 254) reviewed Vokes's (1973, pp. 97-101) observations concerning the species of *Bursa* found in the Chipola Formation. It was his conclusion that the Chipola specimen identified as *Bursa ("Tutufa") pelouatensis* [now listed as the new species *Bursa (Bufonariella) chipolana*] should be placed in the subgeneric group *Bufonariella*. He based this decision on the fact that the Chipola specimen showed close affinities to two Recent species of *Bufonariella, B. caelata* (Broderip) and *B. granularis* (Röding).

In her paper on the Chipola *Bursa*, Vokes (1973, p. 99) also reported that there was a very close similarity between the Chipola *Bursa* identified as *Bursa ("Tutufa") pelouatensis* and the recent *Tutufa (Tutufella) rubeta*. According to Beu (1980, p. 254), there is a distinct difference between the two species and that the similarities cited by Vokes are purely superficial. In *T. rubeta* he notes that all the varices are in alignment down the spire while in the Chipola *Bursa* the varices become unaligned on the last few whorls. In addition, Beu reported that *T. rubeta* has an operculum with the nucleus situated near the center of the height, and a short distance from the abaxial edge, while the Chipola *Bursa* belongs to a group that has an abapically terminal nucleus.

ACKNOWLEDGMENTS

This investigator would like to extend a special note of thanks to Emily Vokes for providing valuable reference material and for her assistance with photographic work. An additional note of appreciation is also extended to Andrew and Greta Murray, Jean-Claude Six, and Daniel Ladon for their loan of Chipola and Aquitaine Basin specimens.

LOCALITY DATA

The following Tulane University localities are all in the Chipola Formation, Calhoun Co., Florida:

546. Tenmile Creek, about 1 3/4 miles west of Chipola River (NE 1/4 Sec. 12, T1N, R10W), (= USGS 2212, "one mile west of Bailey's Ferry").
547. West bank of Chipola River, about 1/2 mile below Tenmile Creek (SW 1/4 Sec. 17, T1N, R9W).
951. Tenmile Creek, about 1 3/4 miles west of Chipola River (SE 1/4 Sec. 12, T1N, R10W).
1051. Tenmile Creek, south bank just downstream from TU 817 (SE 1/4 Sec. 12, T1N, R10W).
1098. Tenmile Creek, south bank just east of power line crossing (SE 1/4 Sec. 12, T1N, R10W).
1196. Farley Creek, north bank about 0.8 mile east of bridge on Florida Highway 275, approximately 500 feet upstream from TU 1048 (NE 1/4 Sec. 21, T1N, R9W).

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August 27, 1997

PLATE 1

Figures

1. *Bursa (Bufonariella) chipolana* Schmelz, n. sp. (X 1-1/2)
   UF 73199 (holotype); height 46.0 mm, diameter 29.0 mm.
   Locality: TU 546, Chipola Formation, Florida.
2. *Bursa (Bufonariella) pelouatensis* (Cossmann and Peyrot, 1923) (X 1-1/2)
   Daniel Ladon collection; height 46.8 mm, diameter 29.9 mm.
   Locality: Saucats (Pelova), France.

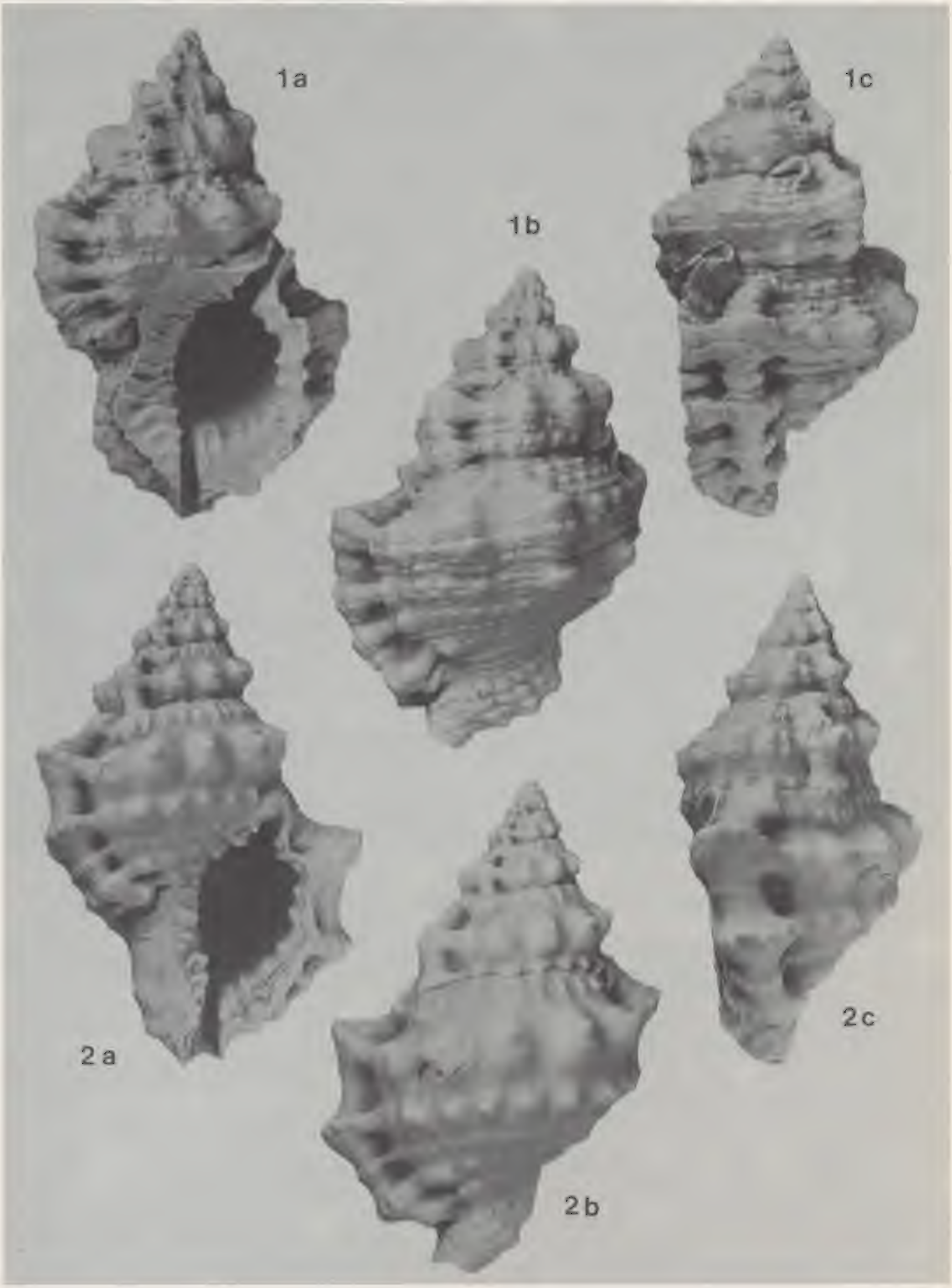

PLATE 1

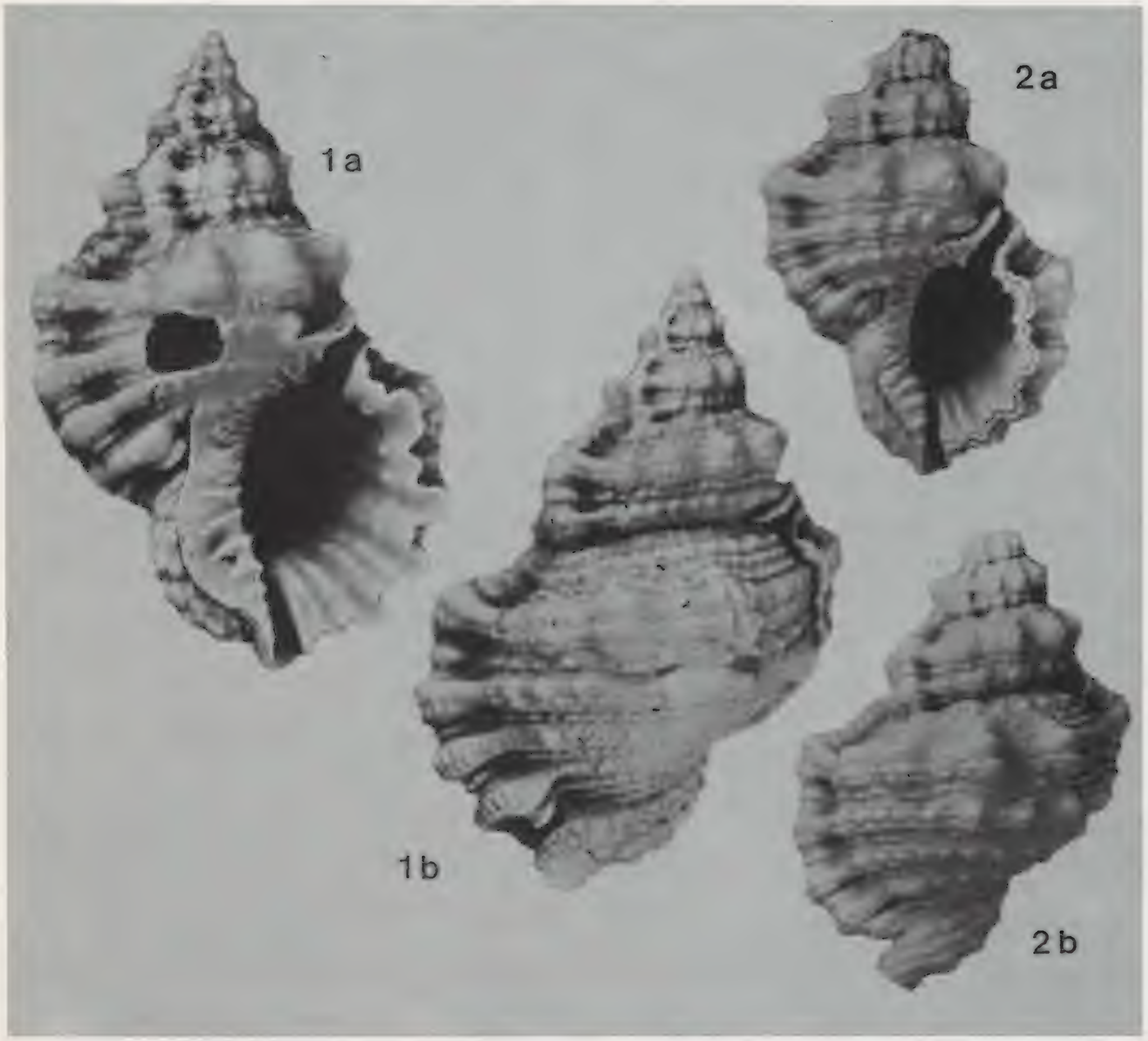

PLATE 2

Figures

1, 2. *Bursa (Bufonariella) chipolana* Schmelz, n. sp. (X 1-1/2)

1. USNM 647108 (paratype Á); height 48.3 mm, diameter 30.8 mm. Locality: TU 547, Chipola Formation, Florida.
2. UF 73200 (paratype B); height 35.0 mm, diameter 24.2 mm. Locality: TU 951, Chipola Formation, Florida.

TRAIL-PRODUCING BEHAVIOR OF *OLIVA SAYANA* (GASTROPODA) IN THE LOWER FORESHORE AT BOGUE BANKS, NORTH CAROLINA

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ABSTRACT

Olive snails living on a very low-gradient, fine to medium sand substrate in the lower foreshore at Pine Knoll Shores produced two kinds of surface trail. Most olives made short, straight to slightly curved trails only a few 10's-of-cm's long, then dived below the surface pushing up a crescent-shaped pressure ridge of sand ahead of the shell. A few snails, however, including some that were experimentally exhumed, prolonged their surface exposure and produced elaborate trails > 100 cm in length. Prolonged exposure often was related to disturbance: exhumed snails wandered across the beach during low tides in an attempt to locate wet, soft sand for reburrowing, and sometimes "floundered" when suitable substrate could not be located. Trails made in this way have wide-looping sections followed by circling/meandering parts. Some snails may have been simply "dawdling", but none of the olives observed, during daylight at this location, seemed to be searching for food. Although interpretation of shapes of trails in plan view is problematic (as would be the resulting trace fossils), cross-sectional shape of the trails is clearly a result of water content and firmness of the sand substrate. Trails having V-shaped cross sections and indistinct marginal levees were produced in soupy sand; U-shaped cross sections having overarching upper limbs were made in wet, firm surfaces; and rectangular cross sections with discontinuous levees were produced by olives moving over dry, hard sand.

INTRODUCTION

We are accustomed to thinking of the phenotypic properties of invertebrate animals, including behavioral systems represented in trace fossils such as burrows and trails, as being wholly adaptive or efficient. If the behavior of organisms were not efficient, the expected results should include reduced fitness, competitive displacement, and exposure to predation. Behavioral aspects of phenotypes ought to be solutions to problems of staying alive in the short run, and ultimately a means of leveraging genes into subsequent generations. This is largely true, but certain activities of organisms do not appear to be efficient uses of energy or adaptively advantageous. Part of this apparent inefficiency results from organisms finding themselves in situations not accommodated by their behavioral programs, and part could be owing to the fact that not all behavior has an immediate, adaptive application. Using human-related metaphors, the former would be floundering, and the latter is a kind of dawdling.

In June, 1995, I observed the trail-producing behavior of *Oliva sayana* Ravenel, 1834, on the ocean beach at Pine Knoll Shores, approximately 15 km west of Beaufort Inlet on Bogue Banks (Fig. 1). The locality has been described by Miller (1995). Specifically, I photographed olives on a very low-gradient, fine to medium sand substrate, in the lower foreshore during a series of low tides (Fig. 2). I also induced the snails to produce traces by exhuming them. Olives appear to be confined to such low-gradient, relatively lower-energy sandflats in this area.

OLIVA SAYANA AT PINE KNOLL SHORES

Olive shells are a familiar component of shelly deposits on North Carolina beaches in the vicinity of Cape Lookout. Living specimens of *O. sayana* are found on exposed and protected sand beaches and intertidal flats (Pearse *et al.*, 1942; Abbott, 1968, 1974; Porter, 1974; Gosner, 1978; Dover and Kirby-Smith, 1979; Meyer, 1994; Abbott and Morris, 1995). Although the largest populations are located in lower intertidal to shallow subtidal environments, a few records have the species in deeper subtidal settings (see Porter,

1974; Dover and Kirby-Smith, 1979). The snail is a motile, shallow-burrowing predator/scavenger that often occurs in localized aggregations or patches (Olsson and Crovo, 1968; Dover and Kirby-Smith, 1979; Meyer, 1994). Maximum density of individuals at Pine Knoll Shores was in the order of 0.5 to 2 snails/m^2. Olives have a patchy distribution here, owing to patchiness of suitable substrate, but within patches individuals did not appear to be aggregated. *Donax variabilis* is extremely abundant at the study site and may be the main prey of olives here (Dover and Kirby-Smith, 1979, p. 21). *Oliva sayana* also is a well known component of nearshore Pleistocene deposits in coastal North Carolina (Richards, 1950, 1962; Du Bar *et al.*, 1974). Some of the empty shells on local beaches could be reworked, both from Pleistocene units and from relict Holocene deposits on the continental shelf (Mixon and Pilkey, 1976; Miller, 1995).

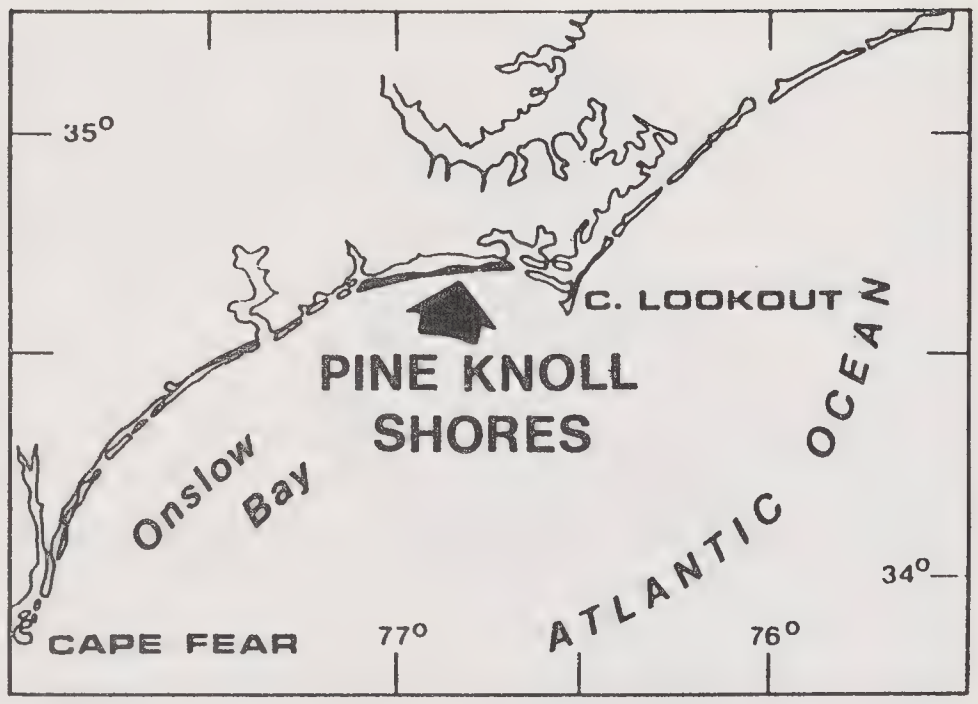

Figure 1. Map showing location of study site on Bogue Banks.

TRACE-PRODUCING BEHAVIOR

There have been few detailed studies of burrowing and trail-making behavior of *O. sayana*. Olsson and Crovo (1968) described behavior of aquarium specimens, emphasizing feeding and reproductive activities. Robert W. Frey and his co-workers mention trails and burrowing behavior of olives in coastal Georgia, as part of their characterizations of modern depositional environments (Frey and Howard, 1969, p. 428-429; Dörjes, 1972, figs. 3 and 4; Howard and Dörjes, 1972, figs. 11 and 14; Howard and Frey, 1980, fig. 21B). These studies documented *O. sayana* as a shallow-tier burrower in beach-related tidal flats and described the species commonly co-occurring with the olives (Frey and Howard, 1972; Howard and Dörjes, 1972). Actual trace-producing behavior was described only generally.

Probably the best description of burrowing was presented over fifty years ago by Pearse *et al.* (1942, p. 150, fig 6). They described the following style of burrowing:

> "Those [burrowing sandflat organisms] that have a very broad foot, secrete much slime, and plunge directly into wet sand (Polynices, Oliva, Olivella, Sinum). These have smooth shells more or less enveloped by the mantle...Oliva [*O. sayana*] has a shiny shell shaped like a torpedo...which readily penetrates sand...A speedy burrower [one specimen of *O. sayana*]...covered itself in 1 minute, 30 seconds..."

They recorded the stages of burrow initiation in a series of photographs taken at 15-second intervals.

Frey and Howard (1972 p. 175, fig. 4) used x-radiographs to show *O. sayana* producing a bioturbate texture in sand. They noted that "...bioturbation by many animals together [including *O. sayana* in the x-radiograph] produces streamy, ropy, or otherwise more irregular textures than those ordinarily seen in cores or other vertical exposures...". In the wet sand of ocean beaches and tidal flats, subsurface burrowing by *O. sayana*, then, is more likely to produce diffuse biodeformation structures than discrete burrows (see Bromley, 1996, p. 8 and 24-25 for description of "intrusion" burrowing causing eddy diffusion patterns and this kind of homogenization of the sediment).

Trail-producing behavior is seldom described in the literature, but is well known to shell collectors. Dover and Kirby-Smith (1979, p. 21) mention that "... olives are predaceous, nocturnal snails... As they move in search of food, they leave a furrowed trail." My observations suggest that feeding behavior is not the only behavioral system resulting in the generation of surface trails.

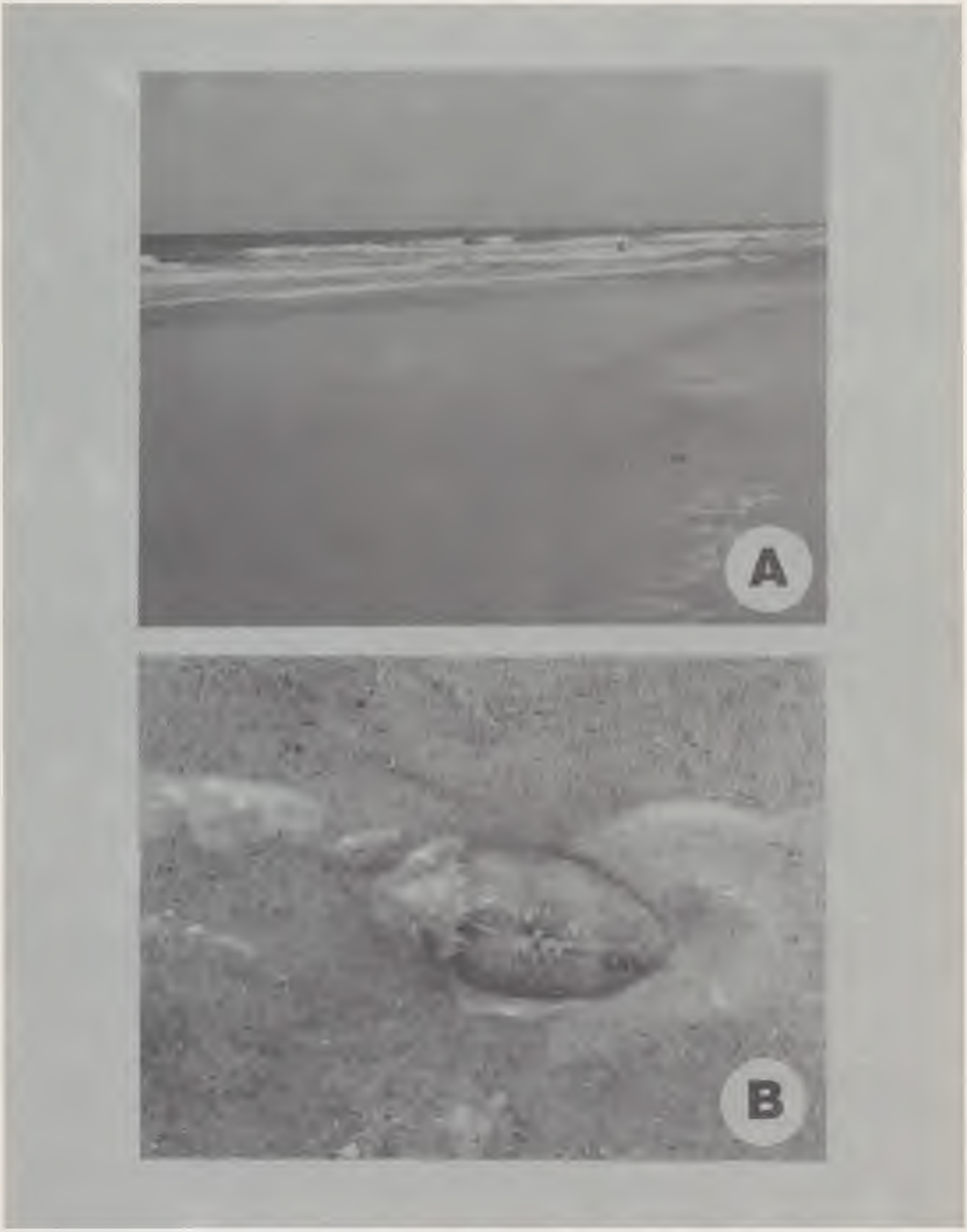

Figure 2. Study site. A, Very low-gradient stretch of beach showing the lower foreshore during a low tide in June, 1995. B, *Oliva sayana* initiating a burrow. Note the large amount of cloudy mucus in the vicinity of the shell and the pressure ridge formed in the sand by the snail diving below the surface. The shell in this photograph, and the shells in Figs. 3 and 4, are approximately 6 cm in length.

OLIVE TRAILS AT PINE KNOLL SHORES

Olive snails are easily located during low tide on nearly flat stretches of beach in the lower foreshore zone. Covered snails were found by locating "dimples" on the surface where olives had recently tunneled into the beach (Fig. 2B). The dimples were produced when snails dived below the surface, pushing up a crescent-shaped pressure ridge of sand ahead of the shell. Most snails dived at angles of 10°-40° relative to the surface and often produced a large quantity of mucus either just before or as burrowing was initiated. Some of the dimples were at the end of trails having varied cross-sectional shapes.

Trails produced in soupy sand were V-shaped in cross section and had indistinct levees (Fig. 3B). In firmer sand, U-shaped furrows were produced having overarching upper limbs (Fig. 3A). These are essentially shallow, horizontal burrows with part of the roof missing. On hard, dry sand, the trails were rectangular in cross section and had irregular, discontinuous levees (Fig. 3C). Water content of the substrate is the primary control of these shapes.

Most of the trails were short, straight to slightly curved structures a few 10's-of-cm's in length, but a few were curved to meandering traces > 100 cm long. At Pine Knoll Shores, during low tides and during daylight hours, most olives attempted to cover themselves without delay to prevent exposure on the sandflat. Presumably, prolonged exposure would increase the chances of encounter with predators (mainly birds at this location) and physiologic stress caused by high temperatures and desiccation. The tendency to reburrow immediately after exposure, however, was not ubiquitous. Some of the snails remained at the surface or were only partially concealed in sand for 10's-of-minutes, while moving across the lower beach. Because potential food such as *D. variabilis* was ignored by the wandering snails, olives apparently were not prolonging exposure to search for food, at least not while I watched them. Olives may have become exposed by localized scour accompanying the falling tide, but it is also possible that they emerge on their own in response to some form of environmental stimulus (indicating a self-initiated a*ction pattern* in the terminology of ethologists [Dawkins, 1986]).

I located several dimples, showing the position of recently covered olives, during three separate low tides, and dug up the snails to observe any trace-producing behavior in response to the exposure. After reorienting their bodies to bring the foot into full contact with the substrate, artificially disturbed olives either produced short trails and then suddenly plunged below the surface, or as described above, they wandered over the sandflat producing long, elaborate trails. Figure 4 shows the trail produced by an exhumed individual that wandered over the sandflat rather than reburrowing immediately. The consistency of the sand substrate was changing rapidly, from firm and wet to hard and dry, during the interval of the three photographs (30 - 40 minutes). The snail was exposed over 10 times longer than the individuals that reburrowed quickly, and produced a composite trail having an earlier wide-looping part (featuring U-shaped cross sections) and a later circling to tightly meandering part (having rectangular cross sections) centered at the middle of the trail system. The long axis of the wide-looping section was oriented more or less perpendicular to the trend of shoreline, suggesting that the snail was prolonging exposure and producing the long trail while trying to locate soft, wet sand for reburrowing. Not all of the long trails at the same location were oriented in this way. On essentially flat areas of the beach, disturbed olives may not be able to judge direction to the ocean and wetter substrates. As the substrate became dry and hard, the snail in Figure 4 produced the circling and meandering part of the trail. This pattern seems to record searching for wet sand, followed by an interval of "floundering" when suitable substrate had not been located.

Snails produced the elaborate surface trails when they were exposed for long periods of time, but it was not always clear why the snails postponed reburrowing in the first place. The long, complex trails are not necessarily related to feeding behavior. Such structures in certain

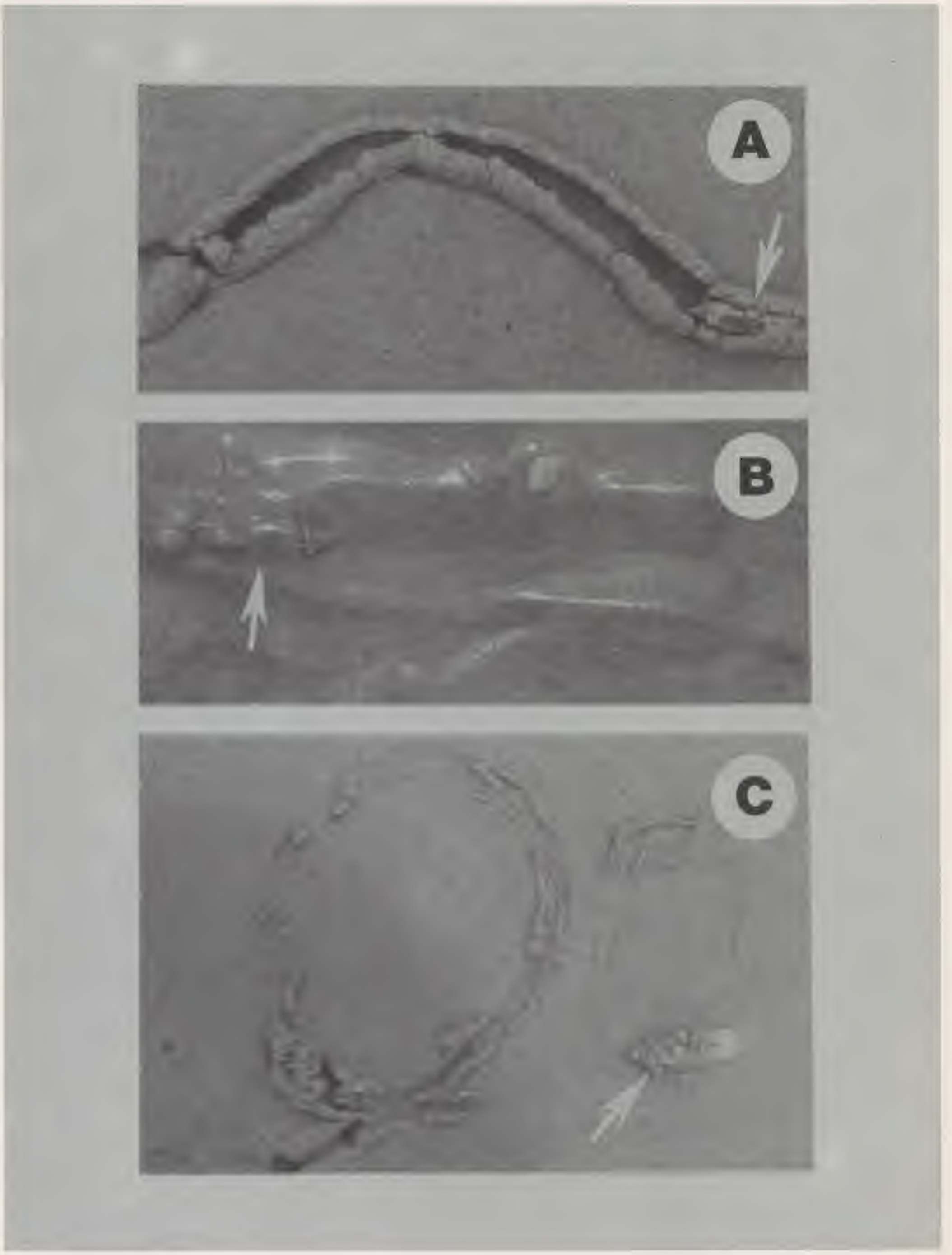

Figure 3. Substrate consistency controlling cross-sectional shapes of surface trails. A, U-shaped in wet, soft sand. B, V-shaped in soupy sand. C, Rectangular cross sections in dry, firm sand. Arrows indicate position of the olives.

cases seem to represent reaction to disturbance (being exposed at the surface) and a fruitless attempt to locate a suitable place to reburrow in wetter, softer sand (Figs. 3C and 4). Long trails produced in soft, wet sand, which were not made by snails searching for food, have no obvious function or purpose (Fig. 3A).

POTENTIAL TRACE FOSSILS

Surface trails like the ones made by *O. sayana* in the lower foreshore at Pine Knoll Shores are likely to be destroyed by erosion. Populations of the same species living on more protected sandflats in the same area, however, could produce preservable structures (see Dover and Kirby-Smith, 1979, p. 8-9). Ichnologists would identify such trails with ichnogenera such as *Archaeonassa* or possibly the all-inclusive *Scolicia* (see Buckman, 1994). From a paleoethologic point of view, wide-looping trails would suggest *repichnia* (locomotion) or *pascichnia* (grazing activity); circling or meandering trails would be interpreted as *pascichnia* or *praedichnia* (referring to predatory behavior). The olive trails that I observed apparently were neither ordinary repichnia nor were the trace producers searching for food, at this particular time and place. Although trail cross-sectional shapes would record water content and substrate consistency unambiguously, overall shape of trails in plan view could reflect reaction to disturbance or something akin to volition *as well as* ordinary movement and feeding activity.

ACKNOWLEDGMENTS

I thank Mr. and Mrs. Daniel Leitch, III, for their generous hospitality at Pine Knoll Shores. Rosemary Hawkins typed the manuscript. A special acknowledgment is due to Dr. Emily H. Vokes, my friend and mentor, for keeping this interesting, high quality journal alive and well for three decades.

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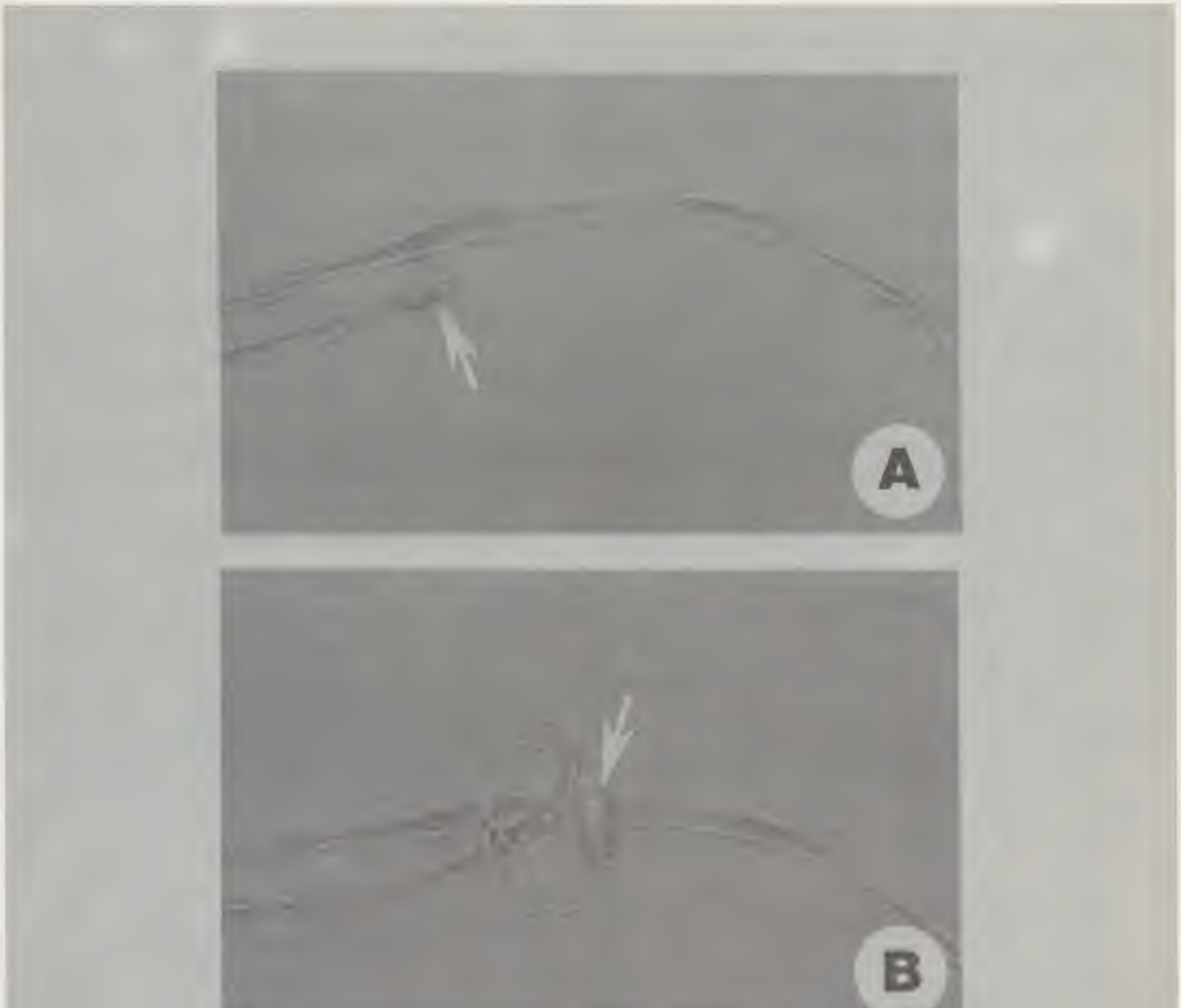
Figure 4. Olive exhumed during low tide producing a long, elaborate trail rather than reburrowing immediately. A, Generation of wide-looping trail. B, Initiation of circling/meandering pattern. C, Position of olive (arrow) at end of composite trail after 30 - 40 minutes of surface exposure.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IS *BATHYSIPHON AALTOI* MILLER, 1986 THE LARGEST FORAMINIFERID?

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Species in the genus *Bathysiphon* are among the largest foraminiferids ever described. Bathysiphonids produce tests that may surpass the size of the associated metazoa (*e.g.*, Gage and Tyler, 1991; Gooday *et al.*, 1992). Large fossil tests also have been described (Miller, 1991, 1995). The tests are agglutinated, simple cylinders, often tens-of-centimeters long and several millimeters in diameter. Most of the modern species occur in deep marine environments at bathyal to abyssal depths. Fossil species are mostly restricted to off-shelf, basinal, and flysch deposits. Loeblich and Tappan (1988) give the geologic range for *Bathysiphon* as Upper Triassic to Recent; Conkin and Conkin (1977, text-fig. 1) extend the range of the genus back to the Middle Ordovician.

In 1986, I described a new bathysiphonid from mid-Cretaceous turbidite deposits in northwestern California. *Bathysiphon aaltoi* was originally described based on fragmentary specimens, which nonetheless suggested that the tests of this species were very large. Additional collecting at the type locality produced a nearly complete test 96 mm long and 3 - 4 mm in diameter (Miller, 1991). The collecting site was neglected for several years, but was revisited in March, 1997. During this latest visit, Mr. Richard Buckhart discovered the largest specimen yet: an *incomplete* test 124 mm in length and 4 mm in maximum diameter (Fig. 1). The original test may have exceeded 150 mm in length, making it one of the largest foraminiferids ever discovered. In this note I document this giant protistan skeleton, and consider some of the implications of its size and occurrence.

Locality: The new specimen was found by splitting open a float block of dark gray mudstone located in the base of a talus slope, on the west side of the quarry road 500 meters south of the old Coast Guard Station on Point Saint George, southwest quarter Crescent City 7.5' quadrangle, coastal Del Norte County, California. The block containing the test was derived from an upslope outcrop of interbedded sandy and muddy turbidites assignable to Facies D in the traditional classification of Mutti and Ricci Lucchi (1978). The thinly-laminated mudstone source rock would be considered a D2 or E2 deposit in the more recent classification of deep marine sediments (Pickering *et al.*, 1989). The fine-grained turbidites in the upslope outcrop probably represent an interchannel basin within a large, dominantly sandy fan system on the mid-Cretaceous seafloor. The deposits are now part of the Yolla Bolly terrane, one of about a dozen tectonostratigraphic divisions of the Franciscan Complex in northern California. Age and origin of the Franciscan rocks at Point Saint George have been discussed by Aalto (1989), Aalto and Murphy (1984), and Miller (1993).

Specimen: The specimen is a typical example of *B. aaltoi*, but very large (Fig. 1). As mentioned earlier, the test was at least 124 mm long. It is up to 4 mm wide, but has been flattened parallel to sedimentary layering so the original diameter can not be determined accurately. The specimen is incomplete, having the narrower, immature end (terminology of Miller, 1995, fig. 2) broken off. A total original length of 150 mm or slightly more is not at all unreasonable.

The specimen is straight, cylindrical, and features the axial striae typical of this species. The test has been flattened parallel to sedimentary layering and resembles a figure-eight in cross section. It was not possible to determine test wall thickness or lumen diameter from the specimen. Parallel, slightly diagonal fractures pass through the test at intervals of 2 - 6 mm, sometimes coinciding with slight constrictions in test width. Although the constrictions may be the same as the irregularities in test diameter mentioned in the literature of fossil and modern bathysiphonids,

the fractures clearly are diagenetic features. As described by Miller (1991, 1995), specimens of *B. aaltoi* are composed of microcrystalline quartz, but originally consisted of spicules and mineral grains.

Significance: The discovery of a bathysiphonid specimen of this size has a number of implications. The test was very large, and ranks among the largest of foraminiferid tests ever discovered. Previously, among fossil bathysiphonids, *B. palachei* (Ulrich, 1904), from the Late Cretaceous of southern Alaska and possibly other areas in the western Pacific, appeared to be the largest bathysiphonid with specimens up to 97 mm long (test originally 120 mm?; Miller, 1995, table 1). The largest living bathysiphonid may be the western Pacific species *B. lanosum* Saidova, 1970, which was reported to be up to 120 mm long (Saidova, 1970, p. 144). Recently, Gooday *et al.* (1992, pls. 5, 6) illustrated living specimens of *B. filiformis* M. Sars, 1872, in the western Atlantic Ocean having up to 10 cm of the test protruding from the seafloor. In the series of specimens they retrieved from bathyal depths off North Carolina, the largest was 119 mm long. If *Bathysiphon aaltoi* is not the largest foraminiferid volumetrically, it certainly ranks as one of the largest in terms of test length.

Another implication relates to living position of *B. aaltoi* and preservation of large tests in mud turbidites. In my study of the paleoecology of *B. aaltoi*, I concluded that the living position most likely was vertical with respect to the seafloor, with the wider, mature end of the test protruding from the substrate and the thinner, immature end positioned in a small pit (Miller, 1988, 1993). In sand turbidites at point Saint George, small immature test fragments can be observed within scoured, plug-like burrows exposed on the soles of the turbidite beds (Miller, 1993). Short barrel-shaped pieces of tests and longer test fragments, which are obviously transported and in some cases concentrated as density-graded lags, can be found within sandstone layers. The largest tests, however, typically occur in the mud turbidites oriented parallel to sedimentary layers. The specimens are rarely broken into small segments and could have been toppled by low-energy bottom currents or bull-dozing benthos before burial. Immature ends of tests are rarely seen oriented vertical to sedimentary layering in the mudstone. This suggests the possibility that vertical to subvertical orientation of tests may not be the exclusive living position of *B. aaltoi*. Although most living species are illustrated having an essentially vertical living position, Christiansen (1971, fig. 3) showed an example of *B. filiformis* having a horizontal orientation.

Finally, considering the size of the specimen described here, one is tempted to speculate about the size of the cell body. If the protoplasm occupied only 10% of the length of the test, it would have extended along the lumen for 10 - 15 mm, making the cell body enormous. There are few published illustrations of bathysiphonid cell bodies. Le Calvez (1938, fig. 1) illustrated a large multinucleate cell in the mature end of *B. filiformis*; the remainder of the test was occupied by a "detrital

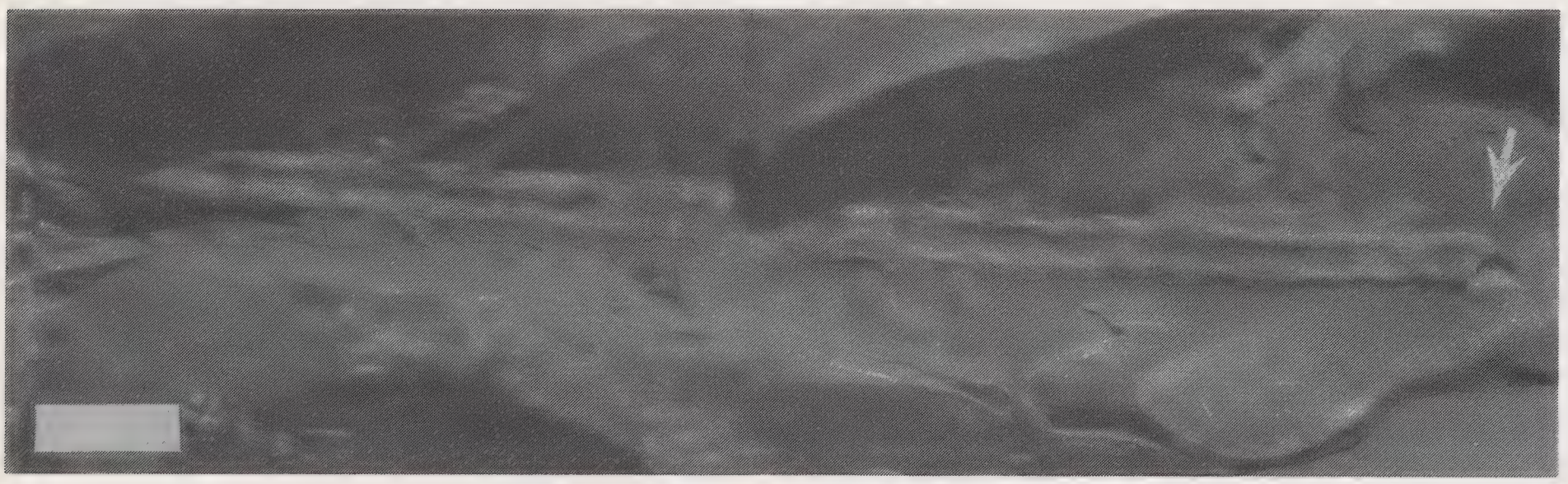

Figure 1. Large *Bathysiphon aaltoi* preserved in a mud turbidite. Arrow indicates broken immature end of test; scale represents 1 cm.

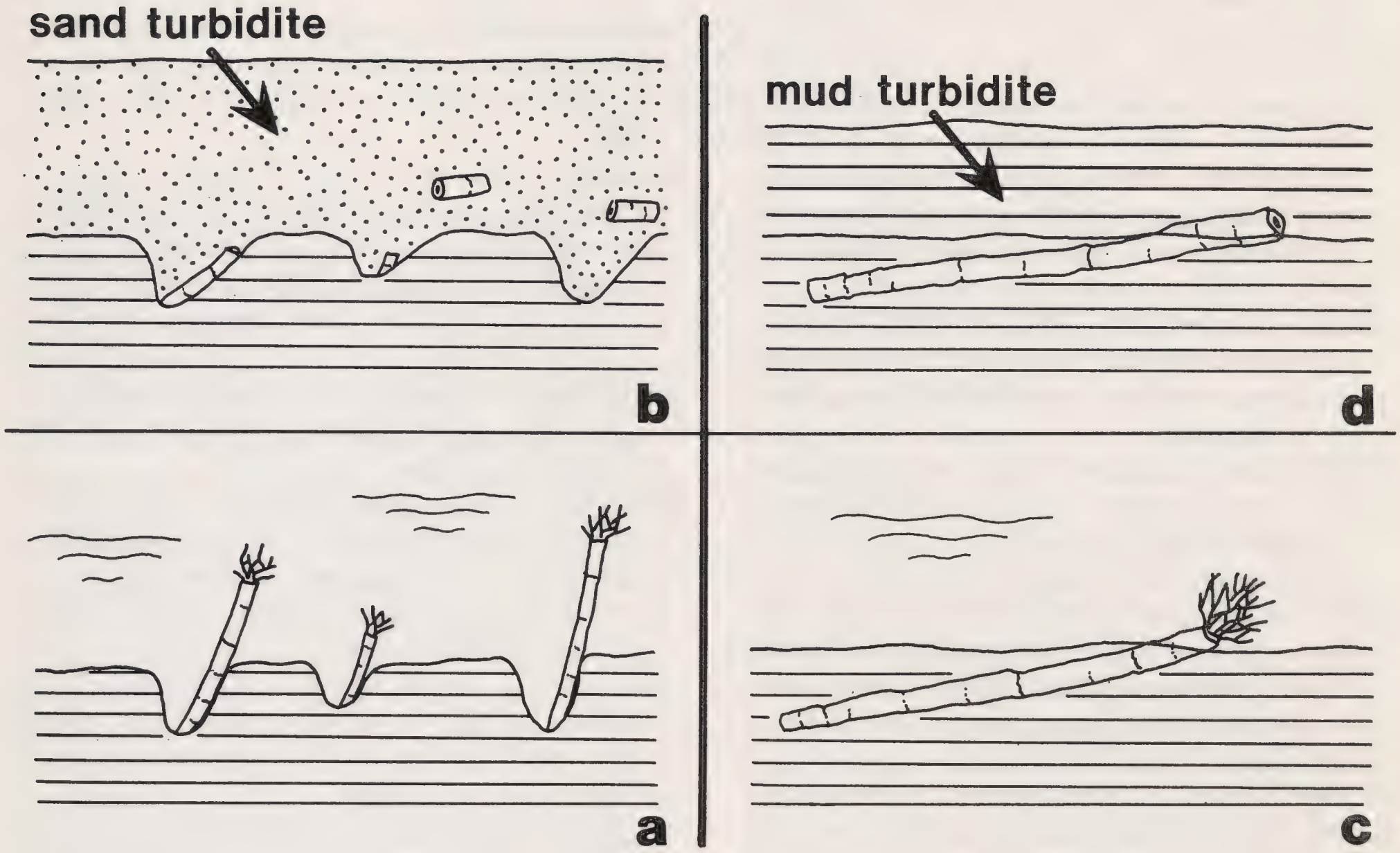

Figure 2. Living positions and preservation of *Bathysiphon aaltoi: a,* subvertical orientation of tests, with the mature ends protruding above the muddy seafloor and the immature ends positioned within a small pit-like burrow; *b,* disturbance and burial by a sand turbidite; *c,* very large test already toppled from the subvertical position; *d,* burial beneath a thin mud turbidite layer (the probable means of preservation recorded in Fig. 1).

plug." The illustration is an idealized sketch, so it is difficult to judge the actual size of the cell body. If the sketch represents the cell body dimensions accurately, the cell extends 9 - 10 mm along the lumen. Gooday (1988, figs. 9B, 11B) illustrated the cell body of *B. major* de Folin, 1886, describing the protoplasm as "... dense, granular and dark grey, sometimes almost black, in colour" (p. 84). In Gooday's figure 11B, the protoplasmic mass or sarcode appears to be approximately 4 mm long. Protoplasmic composition of several species has been illustrated by Gooday and Claugher (1989, fig. 14) and Gooday *et al.* (1992). Certainly, it is not possible to determine the cell-body size of *B. aaltoi*, but considering the overall size of their tests the species may have produced some of the largest protistan cells.

ACKNOWLEDGMENTS

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August 27, 1997

A NEW OCCURRENCE OF THE PROBLEMATICAL FOSSIL *KIRKLANDIA TEXANA* FROM THE CRETACEOUS OF TRANS-PECOS TEXAS

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A fragmentary specimen of the problematical fossil *Kirklandia texana* Caster was collected along U. S. Highway 67 at the town of Shafter, Presidio County, Texas (Text-figure 1). *Kirklandia texana* was originally described by Caster (1945) from the Paw Paw Formation of Denton County, Texas and to date this is the only reported occurrence of this problematical fossil. *Kirklandia texana* has been interpreted as a fossil jellyfish (Caster, 1945) and as a trace fossil (Fursich and Kennedy, 1975). The identification of the Shafter specimen as *Kirklandia texana* Caster was made by comparison to illustrations in Caster (1945) and in Fursich and Kennedy (1975) and by comparisons to the type material at the University of Cincinnati Geological Museum. The occurrence of this specimen of *Kirklandia texana* is interesting in that it is preserved as a cast. Additionally, this is the first reported occurrence of *Kirklandia texana* from the Cretaceous of West Texas and is the only report of *Kirklandia* from the Western Cordillera region.

The specimen was collected from the Lower Cretaceous Shafter Formation of Presidio County, Texas. The section from which it was collected is located on the west side of U. S. Highway 67, 0.5 km south of the intersection with the Shafter town road. This is the type of area of the Shafter Formation. The specific bed from which the specimen was collected is 1.7 m above the base of the outcrop and consists of fine-grained limestone with scattered, small fossil fragments.

No planktonic foraminifera were obtained from the Shafter Formation at this locality and no diagnostic ammonities were collected. Fossils of the benthic foraminiferan *Orbitolina texana* were collected from the Shafter Formation and, based on this, the Shafter is placed within the *Orbitolina texana* benthic foraminifera biozone. This would make the Shafter Formation Early Albian in age and equivalent to the Glen Rose Formation of the Big Bend region to the east (Scott and Kidson, 1977) and to the Bluff Mesa Formation of the Quitman and Eagle Mountains.

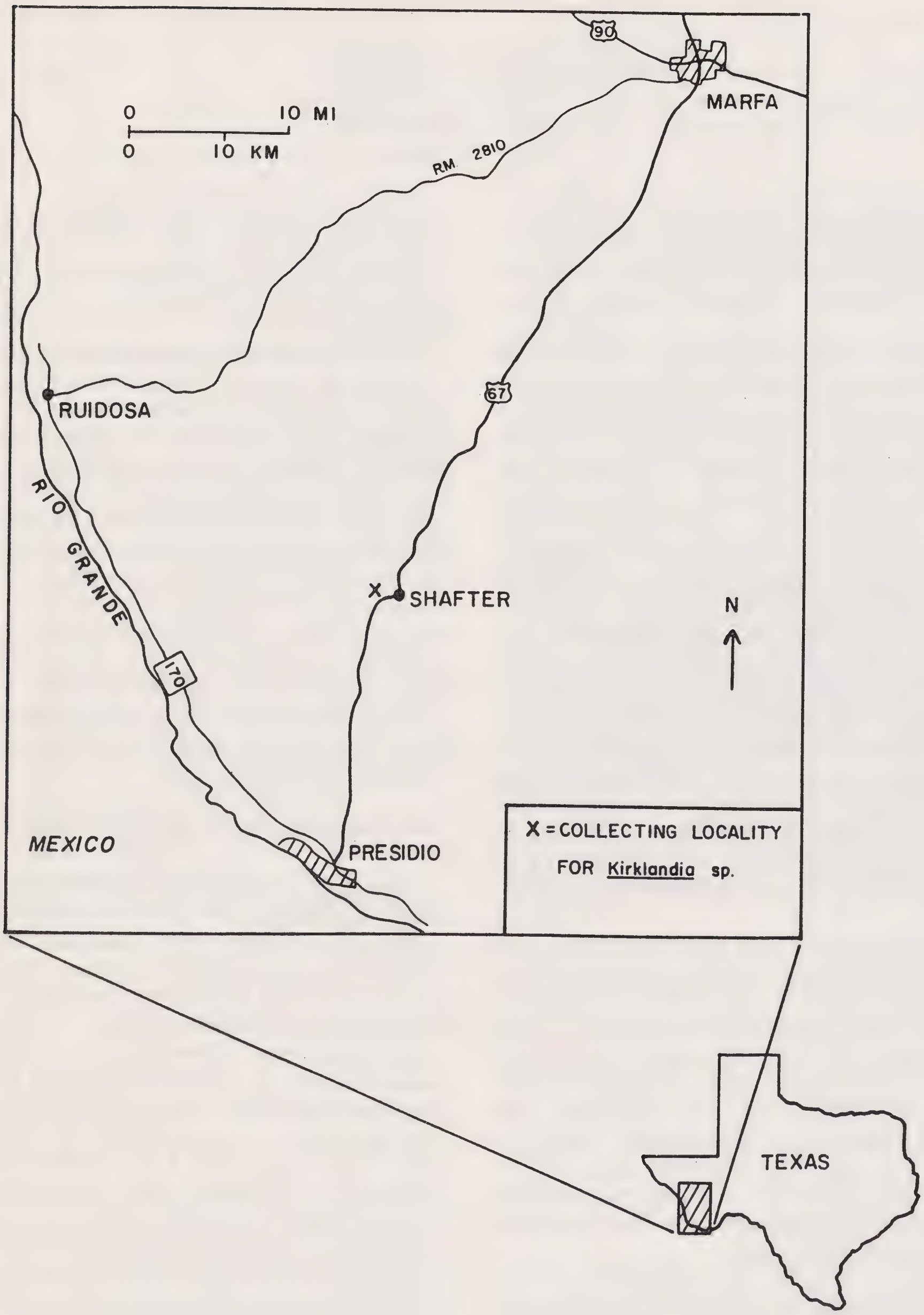
All of the *Kirklandia texana* material studied by Caster (1945) was collected from the Paw Paw Formation of Denton County, Texas. The Paw Paw Formation is latest Albian to earliest Cenomanian in age (Scott and Kidson, 1977, fig. 2). The only other specimens that may be assignable to the genus *Kirklandia* were described by Lorcher (1931) from the Middle Jurassic of Germnay. Given this, the Shafter specimen is the oldest fossil assigned to *Kirklandia* from North America and if the Middle Jurassic forms are not members of the genus *Kirklandia*, then the Shafter specimen is the oldest representative of that genus.

DESCRIPTION OF SPECIMEN

The Shafter specimen of *Kirklandia texana* is housed at the University of Cincinnati Geological Museum (UCGM 46427). For comparative purposes only, the specimen will be described using the nomenclature of Caster (1945).

The specimen is preserved as a partial scalloped disc. It is interpreted as a cast of the subumbrellar surface of *Kirklandia*. The specimen is incomplete, preserving four insert lobes and four swollen protuberances. The texture and composition of the specimen are distinct from the surrounding matrix. No evidence of the paired depressions noted by Caster (1945) is present on the protuberances and no trace of the sulcar star is present. One protuberance does show evidence of a tubular structure, designated a radial canal by Caster (1945). There is also some suggestion of a central elevated structure on the specimen.

One unusual feature of the Shafter specimen that has not been reported from



Text-figure 1. Index map of a part of Trans-Pecos Texas showing the collecting locality for *Kirklandia texana*.

Text-figure 2. *Kirklandia texana* Caster (UCGM 46427). *1.* Photo of UCGM 46427 showing scalloped outline of subumbrellar surface and position of swollen protuberances. Arrow points to detached swollen protuberances. Detail of oral area showing swollen protuberances. Scale bar = .25 cm.

1
2

other *Kirklandia* specimens is the presence of a detached swollen protuberance. This structure is lying upon one of the insert lobes and is about the same size as the other four swollen protuberances preserved on this specimen.

Because the specimen of *Kirklandia texana* from the Shafter Formation is incomplete, a precise measurement of the fossil is not possible. Since the central area is preserved, however, it seems likely that the distance from the edge of an insert lobe to the central area represents a radius of the subumbrellar disc. Therefore, it is possible to estimate the diameter of the original specimen. The measured radius on the Shafter specimen is 20 mm giving an approximate diameter of 40 mm. This value is near the minimum diameter reported by Caster (1945) for the Paw Paw specimens of *Kirklandia texana.*

The specimen of *Kirklandia texana* from the Shafter Formation of West Texas is illustrated in Text-figure 2.

The morphologic nomenclature and the size of the specimens of *Kirklandia texana* from the Paw Paw formation correspond well with the specimen of *Kirklandia* from the Shafter Formation. Given these similarities, the specimen of *Kirklandia* from the Shafter Formation of West Texas is assigned to *Kirklandia texana* Caster.

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A REVIEW OF THE GENUS *CHORUS* GRAY, 1847 (GASTROPODA:MURICIDAE) FROM WESTERN SOUTH AMERICA

THOMAS J. DeVRIES
BURTON, WASHINGTON

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I. ABSTRACT

The muricid genus *Chorus* Gray, 1847, is represented by a single extant species, *C. giganteus* (Lesson, 1830), which lives along the coast of central and southern Chile. New fossils from southern Peru extend the temporal range of *Chorus* from the Pliocene to the Late Miocene (*C. frassinettii*, n. sp.) and the geographic range of three Chilean species [(*C. doliaris* (Philippi, 1887), *C. grandis* (Philippi, 1887), and *C. giganteus*)] into Peru. *Chorus covacevichi*, n. sp., is described from the Pliocene of Chile. Consistent morphological criteria are established for distinguishing all known species of *Chorus*. The genus has been endemic to the Peruvian Province and/or Pacific portion of the Magellanic Province since at least 9 Ma. Extinctions and range contractions of *Chorus* species near the end of the Pliocene may be due to a loss of habitat related to contemporaneous tectonic and oceanographic events.

II. INTRODUCTION

The genus *Chorus* Gray, 1847, is represented by just one living species, *Chorus giganteus* (Lesson, 1830), which has ranged from central to southern Chile (Text-figure 1) since the early Pleistocene (Carcelles, 1954; Herm, 1969; Osorio, 1979). Several Pliocene species have been described (Herm, 1969), all from Chile except one, *C. blainvillei* (d'Orbigny, 1842), which was first discovered in northern Peru and soon afterward found in central Chile (Darwin, 1846).

Miocene and Oligocene species attributed to the genus *Chorus* by Olsson (1931, 1932) from northern Peru and by Arnold (1903) and Anderson (1905) from California are incorrectly identified. Examination of type and figured specimens shows that *Acanthina (Chorus) meroensis* Olsson, 1931, *A. (Chorus) sula* Olsson, 1931, and *A. (Chorus) sula cruziana* Olsson, 1932, are buccinids of

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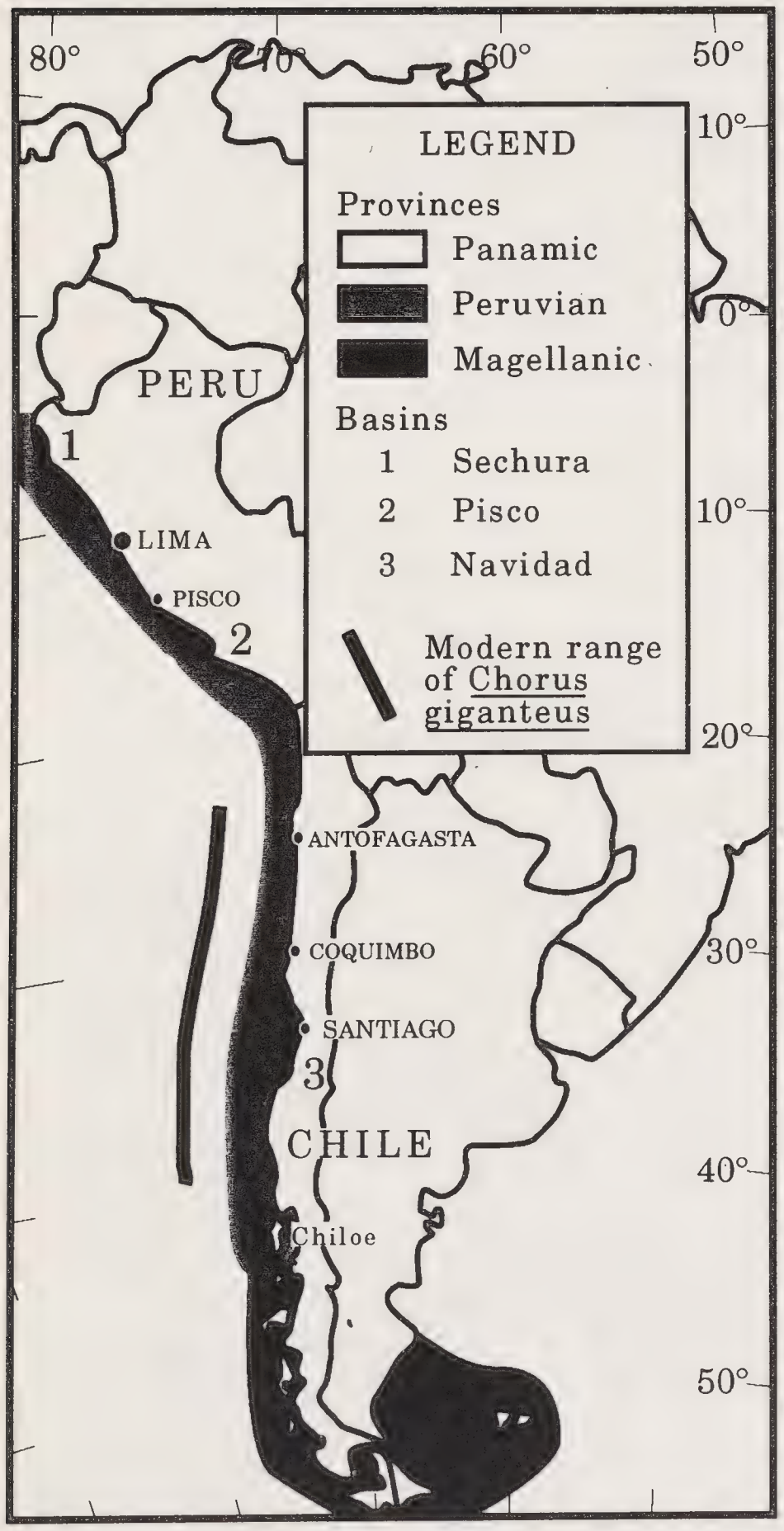


Text-figure 1. The modern range of *Chorus giganteus* Gray, 1847, Quaternary molluscan provinces, and selected Cenozoic sedimentary basins of western South America.

undetermined genera and that *Acanthina (Chorus) voluta* Olsson, 1932, is a pseudolivid (Vermeij and DeVries, 1997). Californian specimens are properly referred to the ocenebrine genus *Forreria* Jousseaume, 1880 (Grant and Gale, 1931).

The classification of *Chorus* within the Muricidae remains uncertain. Gray (1847) created the name for a single species previously assigned to *Monoceros* Lamarck, 1809. He noted similarities with two other muricid genera from the same region, *Nucella* Röding, 1798 (= *Acanthina* Fischer von Waldheim, 1807) and *Concholepas* Lamarck, 1801. *Acanthina* has been assigned to Thaididae Jousseaume, 1888 (*e.g.* Keen, 1971; Abbott, 1974), and more recently, Ocenebrinae Cossmann, 1903 (Kool, 1993; Vermeij and Kool, 1994). *Concholepas* was assigned to Thaididae (or Thaidinae) by Cooke (1919) and Stuardo (1979), but Kool (1993) places it with Rapaninae Gray, 1853. Vermeij and Vokes (1997) consider *Chorus* to belong to a "*Thais*-like" clade of ocenebrines because it has a broadly rounded aperture and no subsutural cord or parietal ridge. *Chorus* differs from most ocenebrines, however, in lacking varices or any other colabral sculpture.

Between 1983 and 1997, field work in the Pisco Basin, an emergent forearc basin on the coast of south-central Peru (Text-figure 1), has yielded an abundance of Late Miocene and Pliocene specimens of *Chorus*. These specimens have been compared with material from the Museo de Historia Natural, Universidad Ricardo Palma (Lima, Peru); examples of *C. blainvillei* collected in northern Peru by the author in 1981 (DeVries, 1986, 1988); and specimens of *Chorus* collected in southern Peru by J. Macharé (formerly with the Instituto Geofísico del Perú) between 1980 and 1984; as well as Chilean specimens in the collections of W. J. Zinsmeister (Purdue University, West Lafayette, Indiana); the California Academy of Sciences (San Francisco); the Museum of Paleontology, University of California (Berkeley); the Museo Nacional de Historia Natural (Santiago, Chile); and the Tavera collection at the Departamento de Geología, Universidad de Chile (Santiago, Chile). The many localities from which these specimens were collected are listed in Part VII and shown in Text-figure 2. Unpublished ^{39}Ar-^{40}Ar dates were provided by L. Snee (United States Geological Survey, Boulder, Colorado).

Study of this material has resulted in the first comprehensive generic diagnosis and description of shell morphology of *Chorus* (see Text-figure 3 for a schematic picture of a *Chorus* specimen); a consistent diagnosis of all known species of

Chorus, including juvenile specimens; and the identification of two new fossil species of *Chorus*.

III. DISCUSSION

Biogeography: The discovery of *Chorus doliaris, C. giganteus,* and *C. grandis* in southern Peru and *C. frassinettii,* n. sp., in both southern Peru and central Chile establishes a minimum range of about 15°S to 36°S for most species of the genus for the Late Miocene and Pliocene. Specimens of *C. blainvillei* from uppermost Pliocene deposits in northern Peru (4°30'S) and *C. doliaris* and *C. giganteus* from Pliocene deposits as far south as 47°S and 45°S, respectively, hint at a wider range for *Chorus*. In contrast, the modern range of *C. giganteus* (23°S to 42°S) is more restricted.

The disappearance of *Chorus* species from low latitudes after the Pliocene is notable for the area affected (1200 km of coastline) and taxonomic breadth (four of four species affected, three of which became extinct), but reflective of biogeographic changes for other muricid genera from western South America. At least one species each of *Acanthina, Concholepas, Herminespina* DeVries and Vermeij, 1997, and *Xanthochorus* Fischer, 1884, lived as far north as 4°30'S near the end of the Pliocene or during the Early Pleistocene (DeVries, 1986, 1988). At present, species of three of those genera do not range so far north, and all species of one genus, *Herminespina,* are extinct.

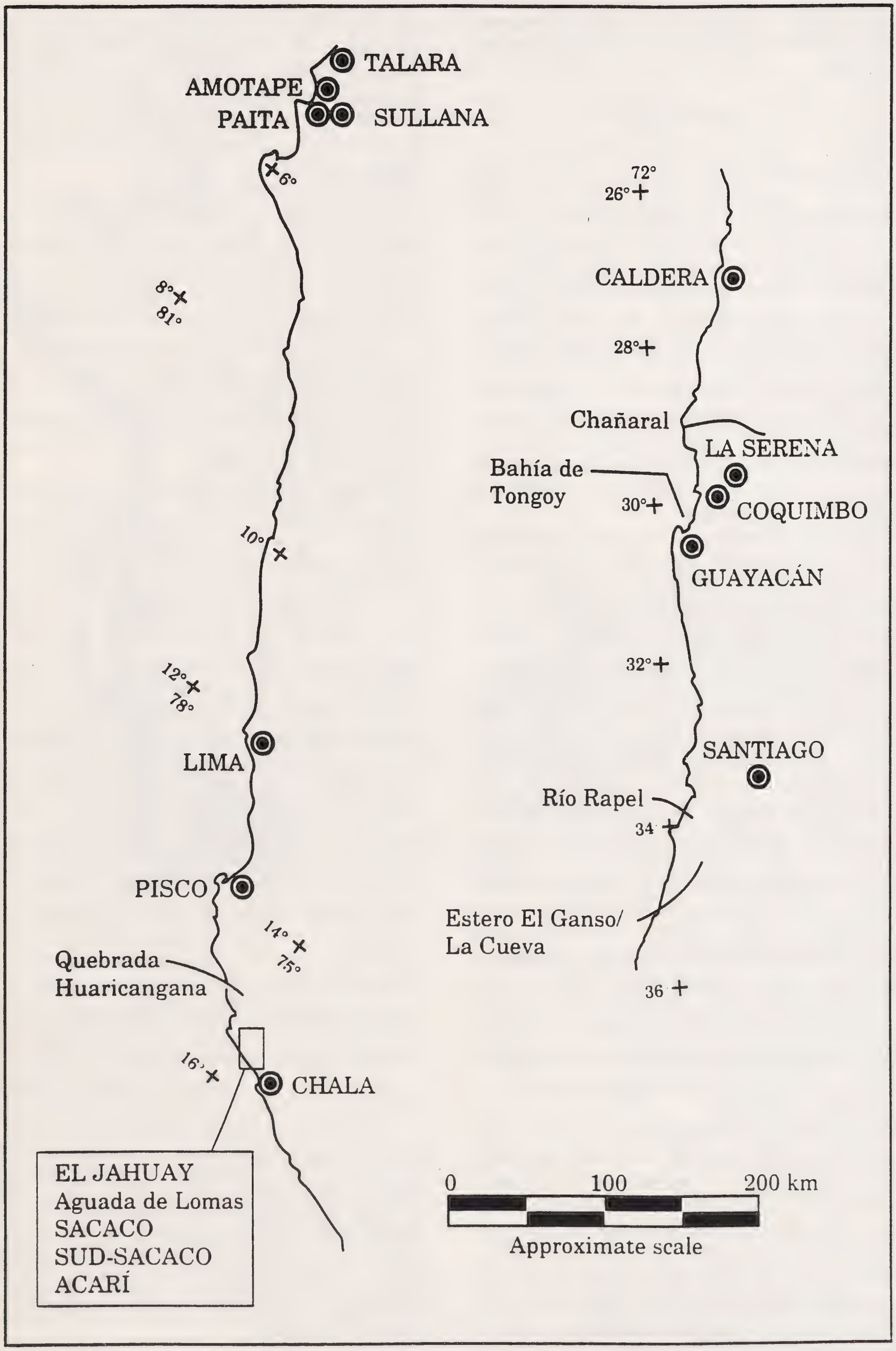
An accelerated loss of molluscan species along the coast of Peru and Chile at the end of the Pliocene has been attributed to a loss of habitat (Herm, 1969; DeVries, 1985). This explanation may also suffice for the extinction and range contractions of species of *Chorus*.

Pliocene and Pleistocene species of *Chorus* in Chile belong to faunal assemblages associated with sandy subtidal substrates along protected and unprotected shores (biotopes 3 and 5; Herm, 1969). In Peru, occurrences of *C. grandis* (localities 87DV 517 and 87DV 569) and *C. blainvillei* (localities 81DV 272 and 81DV 273) in medium-grained sandstones laterally and vertically separated from bioclastic gravels and outcrops of basement igneous rock are consistent with Herm's interpretation. Living populations of *Chorus giganteus* in southern Chile are observed to live subtidally within protected waters, half-buried in muddy sand (Gallardo, 1981).

In contrast, occurrences of *C. grandis* in bioclastic gravels near Chala and *C. frassinettii* in bioclastic conglomerates near Quebrada Huaricangana, in both cases near outcrops of basement igneous rocks, suggest a rocky intertidal habitat. In the latter case, however, deposits of silty sandstone interfinger with the conglomerates. Thus, specimens of *C. frassinettii* could have been transported shoreward from muddy sand substrates onto gravely beaches.

The loss of sandy substrates in protected waters suitable for species of *Chorus* may be attributed to both tectonic and oceanographic events. In both northern Peru and southern Peru, forearc basins that were subsiding during much of the Late Miocene and Pliocene were subject to uplift during the Pleistocene, at the same time that eustatic sea level began to fluctuate dramatically. Protected embayments became emergent and indented shorelines became straight. It may be inferred that, as a result of these changes, *Chorus* habitat became scarce. Refugia may have persisted in southern Chile, in the channels of the Los Chonos Archipelago during sea level high-stands and perhaps within tidally-dominated estuaries during low stands. Fewer high-stand embayments and large rivers are found in northern Chile and Peru, which might explain the disappearance of Pleistocene populations of *Chorus* at those latitudes. Evidence for this hypothesis is provided by the discovery in 1996 of Late Pliocene / Early Pleistocene populations of *C. grandis* and *C. giganteus* in Peru. These populations lived on sandy substrates in the lee of offshore islands and rocky reefs while the margin was still subsiding, and disappeared from the rock record at the same time that the islands were overrun by marine transgressions, which were soon followed by the onset of uplift and rapid sea level changes.

This speculative biogeographic history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AMOTAPE
PAITA
SULLANA
6°
8°
81°
10°
12°
78°
LIMA
PISCO
14°
75°
Quebrada
Huaricangana
16°
CHALA
EL JAHUAY
Aguada de Lomas
SACACO
SUD-SACACO
ACARÍ
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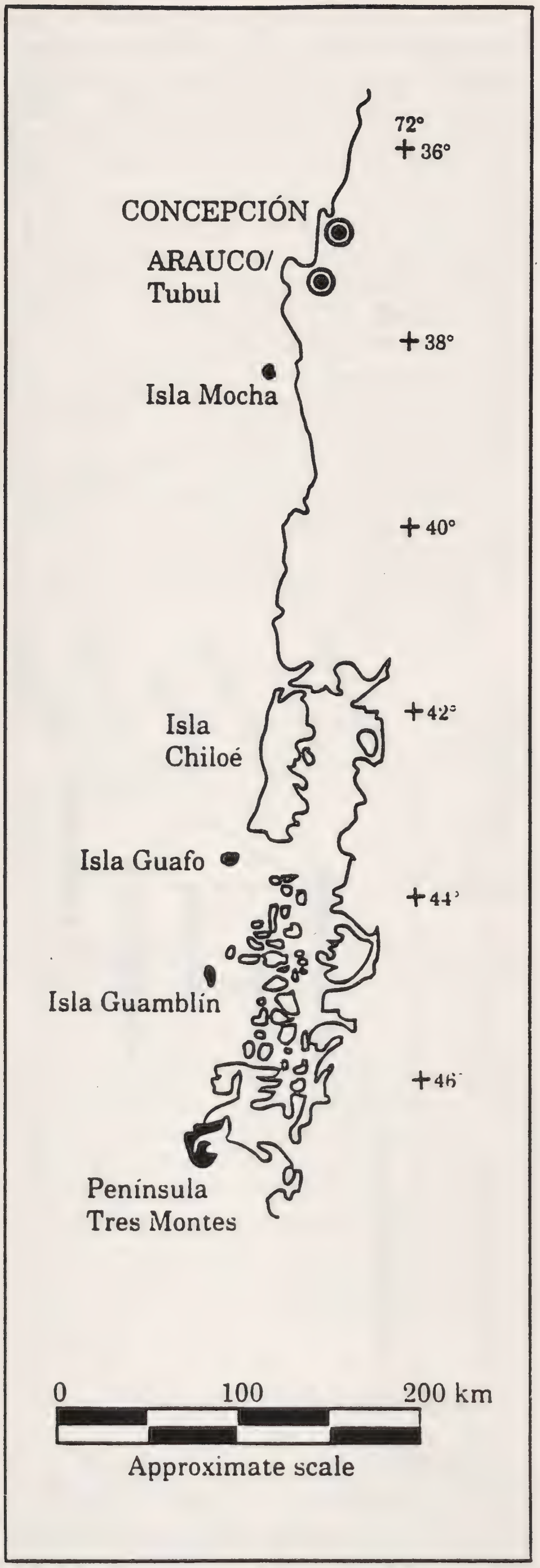


Text-figure 2. Localities from Peru and Chile mentioned in the text.

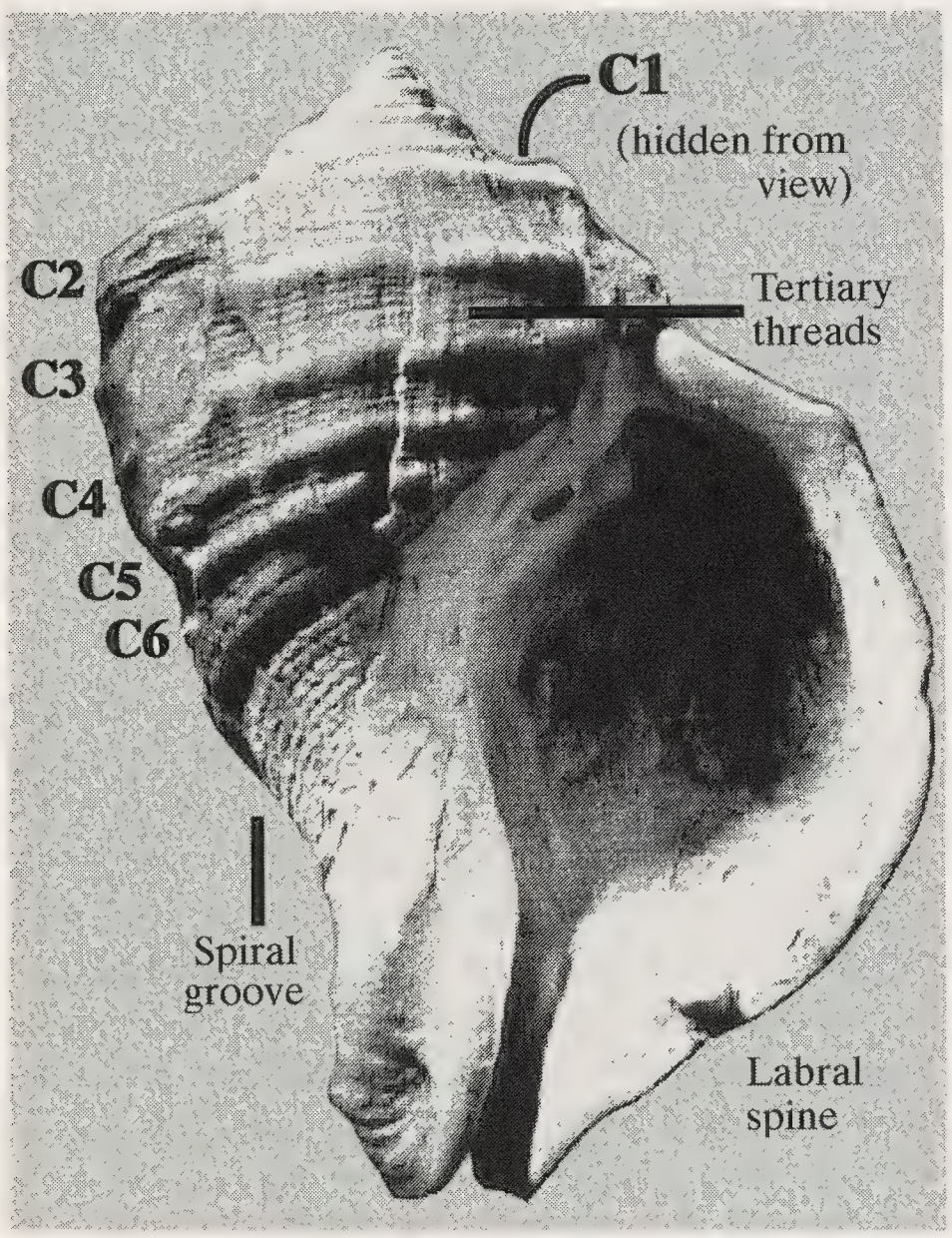
of *Chorus* needs to be tested. Most critical is a better understanding of the ecology of modern populations of *C. giganteus*. Also, Pleistocene deposits with and without *Chorus* need to be mapped in Chile and correlated with independent measures of suitable *Chorus* habitat. Finally, limiting factors other than habitat availability need to be examined for *C. giganteus*, and possibly by proxy, extinct species of *Chorus*: temperature, salinity, prey and predator interactions, competition, and disease.

Phylogeny: The direct predecessor of the genus *Chorus* is not yet known. The oldest species of *Chorus, C. frassinettii*, was already well established from southern Peru to central Chile by the Late Miocene (Text-figure 4). Lower and Middle Miocene deposits from Chile and Peru have not yielded an older species of *Chorus* nor any representative of an older, plausibly related genus.

Chorus frassinettii exhibits a nearly complete suite of *Chorus* characters. The prevalence of well differentiated spiral chords and inflated body whorls in most younger species suggests that uniform spiral sculpture and pyriform shape may be ancestral features. These features reappear in a somewhat different manner in the extant *C. giganteus*. The Pliocene record of intervening extinct species suggests, however, that the superficial similarity of *C. frassinettii* and *C. giganteus* represent convergence.

Chorus grandis is the second oldest species of *Chorus*.. It shares with most younger species an anterior inflation of the body whorl, but is distinguished from all younger species by a preponderance of tertiary threads on the body whorl of adult specimens, a trait it shares with the older *C. frassinettii*. The species appears to have lived from about 6 Ma to 2 Ma. It remains unclear whether Late Pliocene populations of this species or *C. doliaris* gave rise to the modern *C. giganteus*.

Chorus doliaris is a Late Pliocene species that shares with *C. grandis* and *C. frassinettii* the presence of numerous tertiary threads. Unlike those older species, however, the threads never overwhelm the strong primary cords that characterize



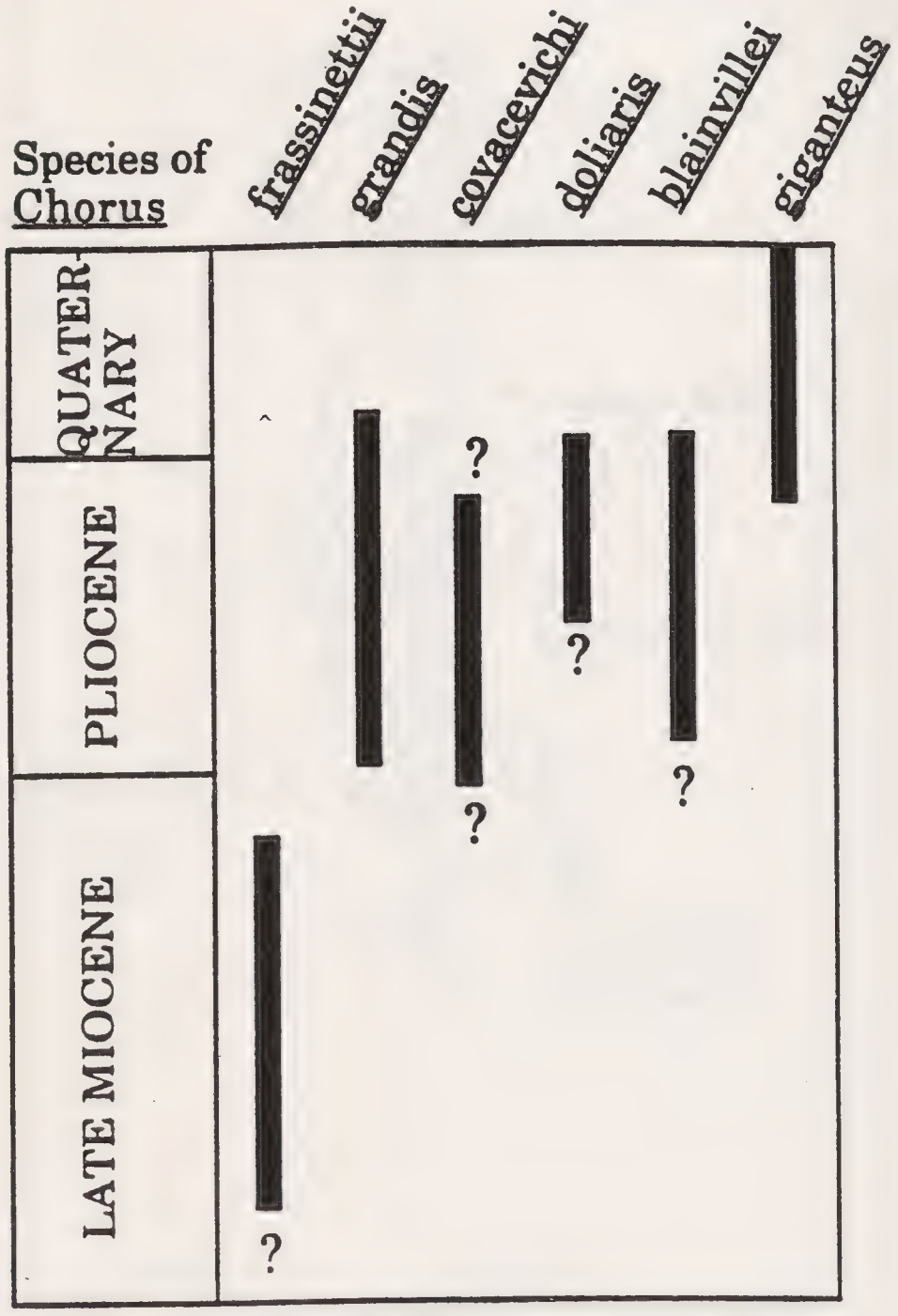
Text-figure 3. Illustration of a *Chorus* specimen to show the numbering scheme (C1, C2, C3, C4, C5, C6) of the primary spiral cords. Primary cord, C1, would be hidden from view in any case, but in this specimen of *Chorus doliaris,* it is absent. Tertiary spiral threads are numerous, whereas secondary spiral cords are absent.

both juveniles and adults. In one Chilean collection, a specimen of *C. doliaris* with greatly reduced anterior inflation and more prominent anterior primary spiral cords is found together with two similar specimens on which the anterior primary spiral cords are even more prominent and the tertiary spiral threads absent, *i.e.,* specimens of *C. giganteus.*

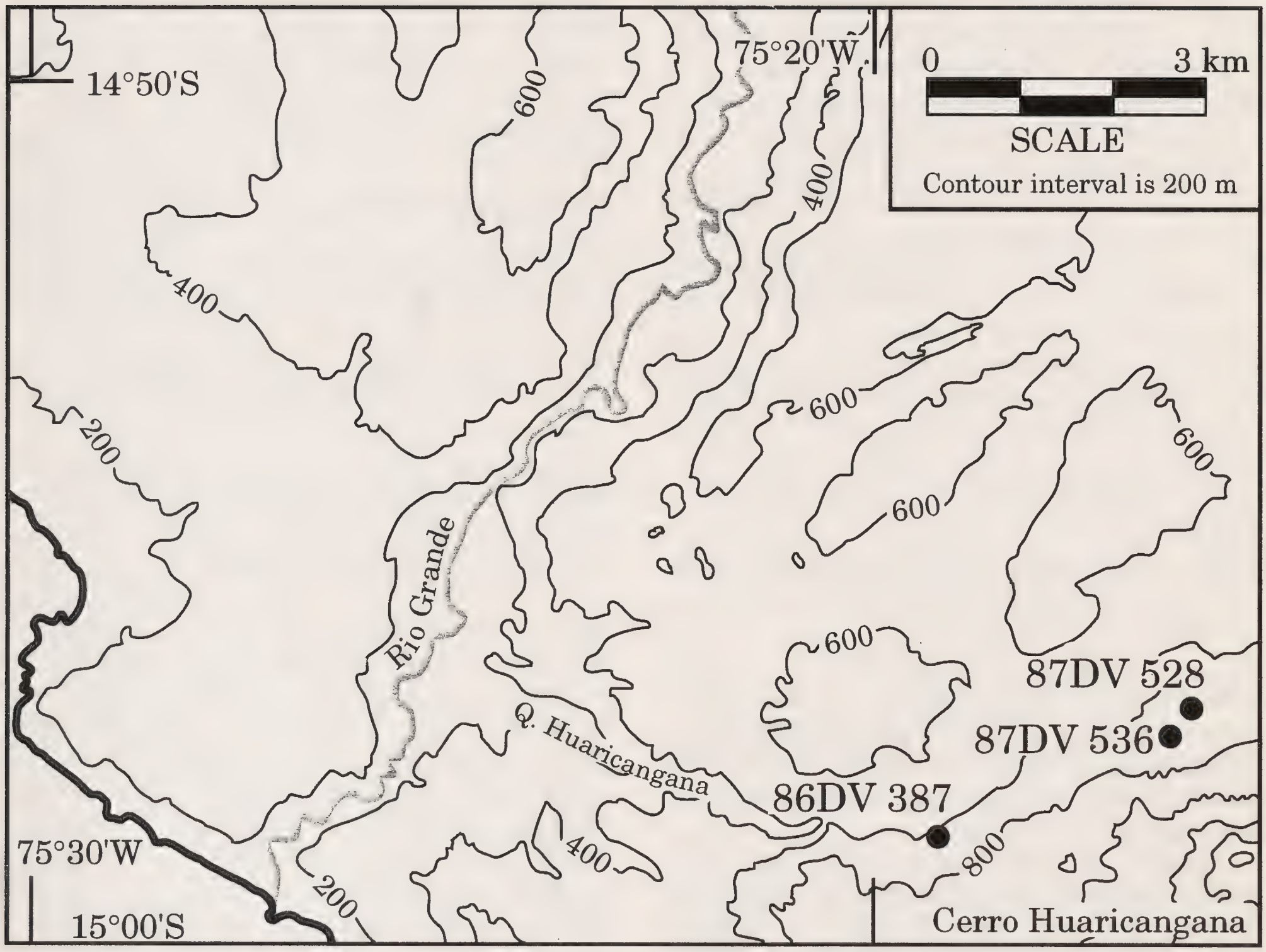
Chorus blainvillei and *C. covacevichi* have only a Pliocene record. Both are characterized by a marked reduction in primary spiral cords in both juvenile specimens (three cords, instead of four) and adult specimens, as well as partial or complete reduction in secondary cords and tertiary threads.

The pattern of morphological traits and first appearances of the above-mentioned species suggests the following phylogenetic history. The genus *Chorus* was represented by successive single species from at least 9 Ma to about 4 Ma. At about 4 Ma, populations of *C. grandis* gave rise to *C. doliaris, C. blainvillei,* and *C. covacevichi.* Somewhat before the time when most species of *Chorus* became extinct, shells of populations of *C. doliaris* or *C. grandis* began converging upon a form similar to that of the much older *C. frassinettii*, producing by the Pleistocene a new morphological species, *C. giganteus.*

This pattern in *Chorus* of slow evolution and low diversity during the Late Miocene and Early Pliocene, radiation during the Pliocene, and extinction near the end of the Pliocene is shared by other western



Text-figure 4. Temporal ranges for species of the genus *Chorus*. A scarcity of dated mollusk-bearing strata between 5 and 4 Ma in Peru and imprecise means for dating bioclastic beds in Chile leaves the earliest appearance of Pliocene species uncertain.



Text-figure 5. Quebrada Huaricangana, south-central Peru, the type locality (87DV 528) of *Chorus frassinettii,* n. sp. Other localities mentioned in the text are shown on the map.

South American muricid genera: *Concholepas, Herminespina,* and to a much lesser extent, *Acanthina* and *Xanthochorus* (DeVries, 1995; DeVries and Vermeij, 1997). Further study of other molluscan genera is needed before persuasive arguments can be advanced to explain the tempo of evolution along the coast of Peru and Chile during the Neogene.

IV. ACKNOWLEDGMENTS

I would like to thank D. Frassinetti (Museo Nacional de Historia Natural, Santiago, Chile) and V. Covacevich (Servicio Nacional de Geología y Minería, Chile) for making collections available for study in Chile and for their helpful critique of the manuscript, and W. Zinsmeister (Purdue University, West Lafayette, Indiana) and G. Vermeij (University of California-Davis) for their reviews of the manuscript. V. Alleman (Universidad Ricardo Palma, Lima, Peru) kindly lent her assistance during a field season in Peru in 1995. R. Martinez-Pardo and E. Valenzuela (Departamento de Geología, Universidad de Chile) arranged access to the Tavera collection. I am grateful to W. Zinsmeister and the several institutions that loaned specimens for this study. Research was funded in part by National Science Foundation Grant EAR-85-03886 and the Conchologists of America, Inc.

Abbreviations for repositories of fossil specimens and localities are as follows:

CAS – California Academy of Sciences, San Francisco, California, U.S.A.
OSU – Orton Museum, Ohio State University, Columbus, Ohio, U.S.A.
RPT – Museo de Historia Natural, Facultad de Ciencias Biológicas, Universidad Ricardo Palma, Lima, Peru.
SGO.PI. – Museo Nacional de Historia Natural, Santiago, Chile.
SU – Stanford University, Palo Alto, California, U.S.A.; now part of CAS collections.
UCMP – University of California at Berkeley, Museum of Paleontology, Berkeley, California, U.S.A.
USNM – United States National Museum of Natural History, Washington, D.C., U.S.A.
WJZ – William J. Zinsmeister, Purdue University, West Lafayette, Indiana, U.S.A.

Measurements of length (l) and width (w) enclosed by parentheses indicate sizes for broken specimens. Descriptions of small juvenile specimens refer to those less than 25 mm long.

Locality data for most samples from collections in Santiago, Chile are listed in the body of the text. Data for other localities are presented in section VII. Most place names are shown on the map in Text-figure 2.

Pagination for Philippi (1887) refers to the Spanish edition.

V. SYSTEMATIC PALEONTOLOGY

Family MURICIDAE Rafinesque, 1815
Genus CHORUS Gray, 1847

Chorus GRAY, 1847, Proceedings of the Zoological Society of London, v. 15, p. 136.

Type Species: (Original designation) *Monoceros giganteus* Lesson, 1830.

Genus Diagnosis: Fusiform, often inflated anteriorly. Axial sculpture of opisthocyrt growth lines; spiral sculpture of six primary cords, wrinkled secondary and tertiary cords, and a V-shaped groove. Some spiral sculpture secondarily lost. Groove ending with labral spine on inside of outer lip, half way between periphery and anterior end.

Genus Description: Length 50 to 100 mm, rarely to 130 mm; fusiform, often inflated anteriorly. Spire low to moderate with five to seven convex whorls; sutures moderately impressed. Shoulder angle and width of sutural platform depending on strength of primary cords. Length of siphonal canal variable between species. Axial sculpture of fine prosocline (angle 40° to 60°), opisthocyrt growth lines with broad apices. Spiral sculpture of three to four primary cords (C2, C3, C4, and C5) at and below shoulder in small juvenile specimens; on larger juveniles and adults, one additional primary cord (C1) near the suture and one to two more (C5, C6) anterior to C4 and posterior to spiral groove. Interspaces sometimes with single secondary spiral cord and numerous tertiary threads. Tiny offsets of tertiary threads along growth lines creating wrinkled texture. Some species with loss of primary, secondary, and/or tertiary spiral cords and threads in adult and, rarely, juvenile specimens. V-shaped spiral groove midway between periphery and anterior end, formed from infolding of outer shell layer at interspace. Neck with numerous flattened spiral threads or cords. Aperture ovate. Parietal area in adults with thin, incomplete, recessed callus. Inner lip straight to concave posteriorly, straight or inclined left anteriorly. Columella smooth, sometimes weakly excavated anteriorly. Pseudumbilical area short. Outer lip nonplanar, non-dentate. Labral spine at end of spiral groove.

Discussion: One of the notable features on specimens of *Chorus* is the labral spine. Other spine-bearing Neogene genera from western South America include *Acanthina* Fischer von Waldheim, 1807; *Testallium* Vermeij and DeVries, 1997; *Herminespina* DeVries and Vermeij, 1997; and *Concholepas* Lamarck, 1801. Individuals of *Acanthina* and *Testallium* are not constricted or only weakly constricted at the base and lack the numerous well-developed primary spiral cords present on specimens of *Chorus*. Specimens of *Herminespina* and *Testallium* have axial sculpture. Specimens of *Concholepas* lack a spiral groove and most species lack labral spines (DeVries, 1995). The pair of labral spines on *Concholepas concholepas* Lamarck, 1801, extend from interspaces, rather than a spiral groove.

CHORUS GIGANTEUS (Lesson, 1830)
Plate 1, figures 1-4; Plate 2, figure 4

Monoceros giganteus LESSON, 1830, p. 405, pl. 11, fig. 4; PHILIPPI, 1887, p. 59.
Monoceros giganteum Lesson. REEVE, 1846, v. 3, pl. 1, fig. 3; HUPÉ, 1854, v. 8, p. 198.
Monoceros fusoides KING, 1832, *in* KING and BRODERIP, p. 348.
Monoceros giganteus ? Lesson. MÖRICKE, 1896, p. 564.
Chorus giganteus (Lesson). CARCELLES, 1954, p. 272, pl. 5, figs. 1-11; HERM, 1969, p. 135, pl. 15, figs. 4a, 4b.
Chorus grandis (Philippi). HERM, 1969, pl. 15, figs. 3a, 3b (not of Philippi).

Diagnosis: No anterior inflation, with rounded shoulder and elongate siphonal canal; strongest primary cords towards anterior, including one or two anterior to spiral groove; tertiary threads absent.

Description: Shell to 130 mm long, fusiform to pyriform; spire about 20 percent of shell length; siphonal canal about 30 percent of shell length. Shoulder rounded, no sutural ramp on large juveniles and adults; periphery just anterior to midpoint between suture and spiral groove. Spiral sculpture of six cords posterior to spiral groove, posteriormost (C1) weak or absent; the next three (C2, C3, C4) moderately strong, with posteriormost (C2) at shoulder; C5 and C6 anterior to C4, more closely spaced and usually stronger than posterior cords. A single secondary cord between C2 and C3, sometimes as strong as adjacent primary cords. Spiral groove situated between two moderately strong flattened cords. Neck of body whorl with one to three moderately strong primary cords and several secondary cords. Tertiary cords rarely developed anywhere on whorl. Pseudumbilical area and excavated anterior end of columella narrow; inner lip concave posteriorly, inclined to left anteriorly. Small juvenile specimens with four strong primary spiral cords (C2, C3, C4, C5), secondary spiral cords between some but not all primary cords.

Type specimen: Unknown.

Type locality: Chile.

Occurrence: (Late Pliocene) southern Peru to central Chile. (Quaternary) central to southern Chile, 23°-42°S (Osorio, 1979; Gallardo, 1981). Late Pliocene ages are assigned on the basis of associated mollusks (Isla Guamblín: Frassinetti and Covacevich, 1995) and position below Pleistocene marine terraces with a modern fauna (Chile specimens: Herm, 1969; Acarí specimens: this report). The two specimens from Acarí constitute the first records of *C. giganteus* of any age from Peru.

Material examined: USNM 447062, locality WJZ 281, Tubul, Pleistocene, l 64.6 mm, w 41.7 mm; USNM 447063, locality WJZ 285, Río Rapel, Recent, l 49.7 mm, w 31.5 mm; USNM 447064, WJZ 659, Isla Guamblín, Late Pliocene, l (38.5) mm, w 26.6 mm; UCMP D-3733c, La Serena, Pliocene, l 127.0 mm, w 82.9 mm; UCMP D-3735a, La Serena, Pliocene, l 38.4 mm, w 24.9 mm; UCMP D-3735b, l 23 mm, w 14.3 mm; RPT 26, Acarí, Late Pliocene, l 41.3 mm, w 29.0 mm; RPT 27, Acarí, Late Pliocene, l (67) mm, w 70.5 mm.

Discussion: A well-formed sutural ramp and absence of primary cords on the neck characterize two Pliocene specimens of *C. giganteus* from Chile (UCMP D-3735a, plate 1, figure 2; UCMP D-3735b, plate 2, figure 4). Additionally, primary spiral cords near the periphery are stronger than the anterior cords. These features are typical of *C. doliaris*. Thus, these specimens of *C. giganteus* may represent populations transitional between *C. doliaris* and Quaternary *C. giganteus*, a hypothesis supported by the occurrence in the same Chilean collection of a specimen of *C. doliaris* (UCMP D-3735c; plate 2, figure 5). On the other hand, undescribed specimens from Upper Pliocene / Lower Pleistocene deposits near Acarí exhibit traits of both *C. giganteus* (produced siphonal canal, differentiated primary and secondary spiral cords) and nearly contemporaneous *C. grandis* from 100 km farther south (numerous tertiary spiral threads, sutural platform; unfigured specimens USNM 447081, USNM 447111), resulting in a morphology convergent with that of *C. doliaris*. Further study is needed to determine the Pliocene species most closely related to the extant *C. giganteus*.

CHORUS DOLIARIS (Philippi, 1887)
Plate 1, figures 5-8; Plate 2, figure 2

Monoceros doliaris PHILIPPI, 1887, p. 57, pl. 6, fig. 11.
Monoceros pyrulatus PHILIPPI, 1887, p. 57, pl. 5, fig. 7.
Monoceros costatus Sowerby. PHILIPPI, 1887, p. 56, pl. 5, fig. 9 (not of Sowerby).

Monoceros cf. *M. pyrulatus* Philippi. MÖRICKE, 1896, p. 566.

Chorus doliaris (Philippi). HERM, 1969, p. 134, pl. 15, fig. 6; pl. 16, fig. 3; pl. 17, fig. 1.

Diagnosis: Moderate anterior inflation and pronounced sutural platform; three strong spiral cords at and below shoulder; tertiary spiral threads filling all interspaces.

Description: Length to 60 mm; fusiform, somewhat inflated anteriorly. Spire, neck each about 20 percent of shell length. Spiral sculpture of large juveniles with six primary cords: three very strong cords at (C2) and anterior to (C3, C4) shoulder; one weak primary cord (C1) on sutural ramp; two moderately strong spiral cords (C5, C6) between C4 and spiral groove; secondary cords and tertiary threads between central or all primary cords. C2, C3, and C4 remaining very strong on adult specimens; C1 and C6 weakening considerably; secondary and tertiary threads becoming stronger, more numerous on adult specimens. Neck with seven to ten tertiary spiral threads, in some cases with one primary spiral cord. Pseudumbilicus and excavated anterior portion of columella wide; posterior inner lip concave; anterior inner lip straight or twisted left. Labral spine inside of outer lip. Small juvenile specimens with four strong primary spiral cords (C2, C3, C4, C5), tertiary spiral threads between all primary cords.

Type specimen: Holotype, SGO.PI.500.

Type locality: La Cueva, Chile.

Occurrence: (Late Pliocene) Southern Peru to southern Chile. Late Pliocene ages are based on associated molluscan fauna and stratigraphic position of specimens (Herm, 1969; Frassinetti and Covacevich, 1995). UCMP and WJZ samples do not specify "early" or "late" for their Pliocene designations.

Material examined: (all samples Pliocene). USNM 447069, locality WJZ 266, La Cueva, l 56.7 mm, w 46.7 mm; USNM 447070, locality WJZ 266, l 28.9 mm, w 22.3 mm; USNM 447071, locality WJZ 848, Isla Guafo, l 58.4 mm, w (40.2) mm; USNM 447072, locality WJZ 848, l (45.9) mm, w (30.0) mm; USNM 447073, locality WJZ 859, Isla Guamblín, Late Pliocene, l 58.3 mm, w (42.0) mm; USNM 447077, locality 82JM 82024, Quebrada Carrizal, l (40.2) mm, w 35.9 mm; USNM 447113, locality WJZ 266, l 18.4 mm, w 13.4 mm; UCMP D-3735C, Coquimbo, l 46.2 mm, w (31.9) mm; UCMP D-5826a, Estero El Ganso, l 24.3 mm, w 18.4 mm; UCMP D-5826b, l 20.9 mm, w 16.1 mm; SGO.PI.1217, Quebrada Salinas, Tongoy, two juvenile specimens; SGO.PI.1303, Estero El Ganso, La Cueva, four adult specimens; SGO.PI.5698, Isla Guafo, two specimens; SGO.PI.5699, Isla Guafo, five adults; SGO.PI.5700, Isla Guafo, one adult. *"Monoceros costatus,"* SGO.PI.517, Guayacán; SGO.PI.841, La Cueva, three specimens; SGO.PI.501, Guayacán, two specimens.

Discussion: The wrinkled tertiary spiral threads and anterior inflation present in

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PLATE 1

Figures Page

1-4. *Chorus giganteus* (Lesson, 1830) 132
1. (x 1) USNM 447062; length 64.6 mm, width 41.7 mm. Locality: WJZ 281, Tubul, Chile; Pleistocene.
2. (x 1) UCMP D-3735a; length 38.4 mm, width 24.9 mm. Locality: Coquimbo, Chile; Pliocene.
3. (x 1) USNM 447063; length 49.7 mm, width 31.5 mm. Locality: WJZ 285, Concepción, Chile; Recent.
4. (x 1) USNM 447064; length (38.5) mm, width 26.6 mm. Locality: WJZ 659, Isla Guamblín, Chile; Late Pliocene.
5-8. *Chorus doliaris* (Philippi, 1887) 133
5. (x 1) UCMP D-3735c; length 46.2 mm, width (31.9) mm. Lateral view; encrusted with barnacles. Locality: Coquimbo, Chile; Pliocene.
6. (x 1) USNM 447071; length 58.4 mm, width (40.2) mm. Locality: WJZ 848, Península Tres Montes, Chile; Pliocene.
7. (x 1.5) UCMP D-5826a; length 24.3 mm, width 18.4 mm. Locality: Estero El Ganso, Chile; Pliocene.
8. (x 1.5) USNM 447070; length 28.9 mm, width 22.3 mm. Locality: WJZ 266, Estero El Ganso, Chile; Pliocene.

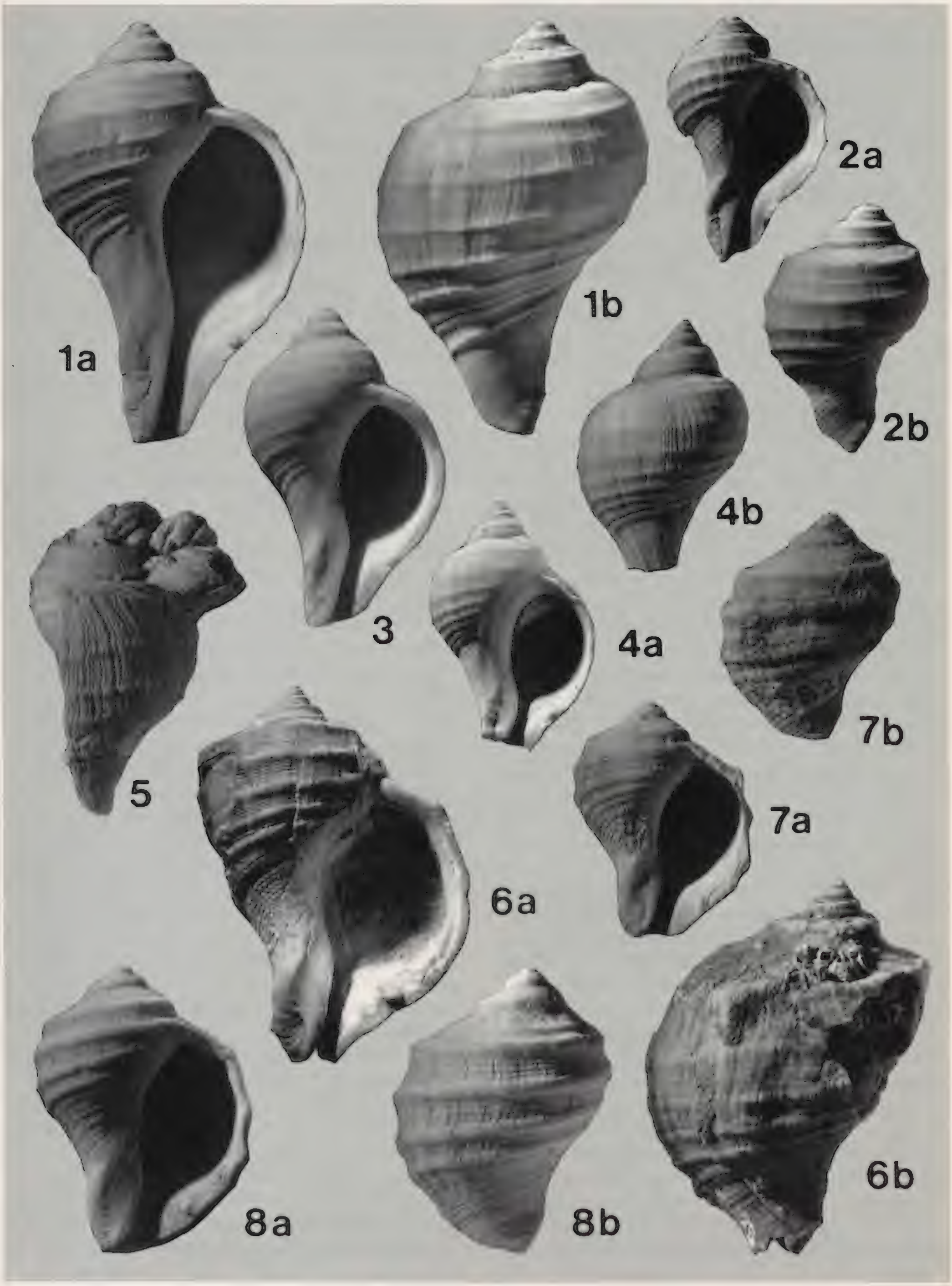

PLATE 1

specimens of *Chorus doliaris* are absent on specimens of *C. giganteus*. Adult specimens of *C. doliaris* have more primary spiral cords than specimens of *C. grandis* and *C. blainvillei*. Nodular specimens of *C. covacevichi* new species lack the tertiary threads seen on noded specimens of *C. doliaris* (Plate 1, figure 6b, and other unfigured specimens that are even more nodulose).

CHORUS COVACEVICHI, n. sp.
Plate 2, figures 8, 9

Diagnosis: Primary cords C1 and C6 weak or absent, others nodulose; tertiary spiral threads absent or nearly absent for all sizes.

Description: Length to 50 mm; fusiform to nearly pyriform, with low spire, narrow sutural platform, adaxially constricted shoulder, inflated body whorl, and moderately elongate siphonal canal; point of maximum inflation anterior to midpoint of body whorl. Spiral sculpture of three very strong primary cords at (C2) and below (C3, C4) shoulder; one moderately strong primary cord (C5) anterior to cord C4; primary cords adjacent to suture (C1) and spiral groove (C6) weak or absent. All primary cords with nodes. Secondary and tertiary sculpture posterior to spiral groove very faint or absent. Neck of body whorl with five to six flattened tertiary threads. Pseudumbilicus and excavated anterior portion of columella wide in adult specimens; posterior portion of columella straight to concave; anterior portion of inner lip straight. Labral spine inside outer lip. Small juvenile specimens with three strong primary spiral cords (C2, C3, C4), smooth interspaces; body whorl constricted at shoulder cord (C2).

Type specimen: Holotype, USNM 447068.

Type locality: WJZ 253, roadcut north of Coquimbo, Chile.

Etymology: This species is named in honor of Vladimir Covacevich C., paleontologist with Chile's Servicio Nacional de Geología y Minería, who has contributed greatly to an understanding of the Tertiary mollusks of Chile.

Occurrence: (Pliocene) central Chile.

Material examined: All material from locality WJZ 253, Coquimbo, Pliocene. USNM 447068, holotype, l (50.1) mm, w 41.9 mm; USNM 447076, paratype, l 26.8 mm, w 19.6 mm; USNM 447118, paratype, l 23.1 mm, w 18.0 mm.

Discussion: Specimens of *Chorus covacevichi*, n. sp., may be distinguished easily from nodular individuals of *C. doliaris* because they lack primary spiral cord C6 and secondary and tertiary sculpture. The nearly pyriform silhouette further distinguishes specimens of *C. covacevichi* from nodular specimens of *C. blainvillei*.

CHORUS GRANDIS (Philippi, 1887)
Plate 2, figures 3, 6, 7; Plate 3, figure 8

Monoceros grandis PHILIPPI, 1887, p. 57, pl. 5, fig. 4, pl. 6, fig. 5; MÖRICKE, 1896, p. 564.
Monoceros laevis PHILIPPI, 1887, p. 57, pl. 5, fig. 8.
Monoceros tenuis PHILIPPI, 1887, p. 57, pl. 5, fig. 10.
Monoceros ventrosus PHILIPPI, 1887, p. 58, pl. 6, fig. 4.
Chorus grandis (Philippi). HERM, 1969, p. 134, pl. 15, figs. 2, 3, and 5.

Diagnosis: Weak sutural platform; tertiary spiral threads predominate, primary cords absent in adults except rarely at shoulder.

Description: Length to 90 mm; fusiform, inflated anteriorly; spire 20 perçent and neck 15 percent of length. Large juveniles with rounded shoulders; adults with weakly sulcate sutural ramp and angled shoulder. Small juvenile specimens smooth or with three to four strong primary spiral cords (C1, C2, C3, C4) becoming low and rounded; interspaces smooth or with faint secondary spiral cords. Insertion of secondary cords, strong tertiary threads, and diminishing primary cords on whorls of large juveniles and adults resulting in pattern of wrinkled, flattened, tertiary threads separated by thread-like incisions on adults; cords C2, C3, and C4 sometimes weakly expressed, other primary cords usually not evident. Second large juvenile morphotype with nearly smooth body whorl posterior to spiral groove. Neck of body whorl with numerous weak, flattened, tertiary threads. Pseudumbilical area and excavated anterior portion of columella deep but narrow; posterior and anterior edge of inner lip nearly straight. Labral spine inside outer lip.

Type specimen: Holotype, SGO.PI.510.

Type locality: La Cueva, Chile.

Occurrence: (Early to Late Pliocene) southern Peru to central Chile. Ages for Chilean specimens described by Herm (1969) are based on associated molluscan species and stratigraphy.

Early Pliocene age assignments for Peruvian specimens (USNM 447074, USNM 447075) are based on radiometrically dated volcanic ashes and diatom assemblages in nearby beds (de Muizon and DeVries, 1985). Late Pliocene ages for Peruvian specimens (USNM 447081, USNM 447111) are based on associated specimens of an undescribed species of *Concholepas* Lamarck, 1801, very similar to the Quaternary *C. concholepas* Lamarck, 1801.

Material examined: All Pliocene. *Chorus grandis:* USNM 447074, sample 87DV 517-1, Sud-Sacaco, late early Pliocene, l 57.6 mm, w 42.0 mm; USNM 447075, sample 87DV 569-1, Sud-Sacaco, l (14.2) mm, w 11.1 mm; USNM 447081, sample 95DV 812-1, Quebrada Huacllaco, near Chala, Late Pliocene, l (84.3) mm, w (52.4) mm; USNM 447119, locality WJZ 385, Coquimbo, l (18) mm, w 13.4 mm; USNM 447111, sample 95DV 812-1, l (89.1) mm, w (61.9) mm; SGO.PI.510, holotype, La Cueva; SGO.PI.1219, four specimens, Herradura de Guayacán; SGO.PI.1243, Chañaral de las Aceitunas; SGO.PI.5592, Estero El Ganso, La Cueva; SGO.PI.1253, Chañaral de las Aceitunas; CAS 61703.01a, Coquimbo, l (37.2) mm, w 26.0 mm; CAS 61701.02, Quebrada Culebrón, Coquimbo, l (30.5) mm, w 22.4 mm; CAS 61702.01, Guayacán, l (34.4) mm, w 25.0 mm. *Monoceros laevis:* USNM 447078, locality WJZ 385, l 35.6 mm, w 26.5 mm; USNM 447079, locality WJZ 385, l 32.7 mm, w 23.9 mm; USNM 447080, locality WJZ 385, l 28.8 mm, w 22.6 mm; SGO.PI.508 002, holotype, Guayacán; SGO.PI.503, Guayacán; SGO.PI.505, Guayacán; SGO.PI.518, Coquimbo; SGO.PI. 5701, Bahía Herradura de Guayacán, near Quebrada La Rosa. *Monoceros tenuis:* SGO.PI.507, holotype, Coquimbo; SGO.PI.511, Guayacán. *Monoceros ventrosus:* SGO.PI.520, holotype, Coquimbo; SGO.PI.516, Guayacán.

Discussion: The smooth-shelled morphotype of *Chorus grandis* was the basis for Philippi's (1887) description of *Monoceros laevis,* for which *M. ventrosus* is synonym. The holotype of *M. tenuis* exhibits characters of both "sculpted" and "smooth" morphotypes.

Adult specimens of *C. grandis* may be distinguished from those of most other species of *Chorus* by the predominance of tertiary sculpture, and from adults of *C. frassinettii*, which also shows predominantly tertiary sculpture, by an anterior inflation of the body whorl and the presence of a sutural ramp.

CHORUS BLAINVILLEI (d'Orbigny, 1842)
Plate 2, figure 5; Plate 3, figures 5, 6, 7

Monoceros blainvillei d'ORBIGNY, 1842, p. 116, pl. 6, figs. 18, 19; DARWIN, 1846, p. 129; HUPÉ, 1854, v. 8, p. 197; PHILIPPI, 1887, p. 58, pl. 5, fig. 2.

Monoceros blainvillei var. PHILIPPI, 1887, p. 58, pl. 5, fig. 3.

Monoceros blainvillei d'Orbigny var. *nodosa*. MÖRICKE, 1896, p. 563.

Chorus blainvillei blainvillei (d'Orbigny). HERM, 1969, p. 133, pl. 15, figs. 1a, 1b; DeVRIES, 1986, p. 585-586, pl. 34, figs. 1, 3, 4, 5, 9, 11.

Chorus blainvillei nodosus (Möricke). HERM, 1969, p. 133, pl. 16, figs. 1, 2; DeVRIES, 1986, p. 586, pl. 34, fig. 8.

NOT *Chorus* aff. *C. blainvillei* (d'Orbigny). WATTERS and FLEMING, 1972, fig. 6-u.

Diagnosis: Broad sutural platform, strong anterior inflation; primary cords 1 and 6 absent; tertiary spiral threads absent in adults.

Description: Length to 80 mm; juveniles fusiform; adults fusiform with marked anterior inflation, low spire, broad sutural platform, and very short siphonal canal. Spiral sculpture of three primary cords at (C2) and below (C3, C4) shoulder; axially aligned nodes in specimens with nodular spiral cords. All specimens lacking primary cords C1 and C6. No secondary cords; in adults, tertiary threads mostly absent posterior to the spiral groove, except for neck, which has about 10-15 tertiary threads. Pseudumbilical area and excavated anterior portion of columella short and very wide in adults, moderately wide in juveniles. Posterior part of inner lip concave, anterior straight or curved slightly left. Labral spine inside outer lip. Small juvenile specimens with three strong primary spiral cords (C2, C3, C4), smooth interspaces; body whorl not adaxially constricted at shoulder cord (C2).

Type specimen: Unknown.

Type locality: Paita, Peru (d'Orbigny, 1842); probably Quebrada Cardo Grande, about 4 km north of Amotape, Peru, DeVries (1986) locality 273, alongside a road, now largely abandoned, that once connected Talara with Sullana and Paita (Text-figure 2). d'Orbigny described material provided by others and suspected to be from

near Paita; Olsson (1932, p. 6) rediscovered the species near Amotape.

Occurrence: (Pliocene) northern to southern Chile. Chilean localities include both lower and upper Pliocene strata; no distinction is made on SGO.PI. sample labels or in Herm (1969). (Latest Pliocene) northern Peru. The occurrence of specimens of *Chorus blainvillei* at the base of the Taime Formation (DeVries, 1988), together with specimens of typically Pleistocene species (DeVries, 1986), suggests a very late Pliocene or early Pleistocene age in the Sechura Basin (Text-figure 1).

Material examined: All OSU specimens are topotypes from upper Pliocene localities 81DV 272 (Quebrada Sogrona) and 81DV 273 (Quebrada Cardo Grande). All other Peruvian and Chilean material of undifferentiated Pliocene. OSU 37351, l 17.5 mm, w 12 mm; OSU 37352, l 32.9 mm, w 23.2 mm; OSU 37353, l 45.4 mm, w 33.2 mm; OSU 37354, l 59.4 mm, w 46.6 mm; OSU 37355, l 75.8 mm, w 66.8 mm; OSU 37357, l 68.9 mm, w 55.3 mm; SGO.PI.513, Coquimbo; SGO.PI.504, Isla Chiloé; SGO.PI.1102, Caldera; SGO.PI.1096, Caldera; CAS 61701.01, Quebrada Culebrón, Coquimbo, 12 specimens; UCMP D-5790a, Caldera, l (52.2) mm, w 41.2 mm; UCMP D-5790b, l (36.3) mm, w 27.7 mm; UCMP D-5790c, l (32.9) mm, w 25.4 mm.

Discussion: Specimens of *Chorus blainvillei* collected from the type locality in northern Peru, as well as specimens found close at Coquimbo, Chile, the type locality of *C. blainvillei nodosus*, show a wide range in the development of nodular primary spiral cords, suggesting that *C. blainvillei nodosus* should be considered a synonym of *C. blainvillei*. Specimens of *C. covacevichi*, n. sp., may be distinguished from nodulose specimens of *C. blainvillei* by their pyriform outline and absence of secondary cords and tertiary threads on even small juvenile specimens.

CHORUS FRASSINETTII, n. sp.
Plate 2, figure 1; Plate 3, figures 1-4

Diagnosis: Rounded shoulder, minimal anterior inflation. Spiral sculpture in juveniles of nearly equally strong primary and secondary cords, in adults, nearly equally strong primary and secondary cords and tertiary threads.

PLATE 2

Figures — Page

1. *Chorus frassinettii*, n. sp.. 138
   (a, x 1.5; b, x 1.6) USNM 447066; length 19.6 mm, width 14.0 mm.
   Locality: 87DV 571-1, El Jahuay, Peru; Late Miocene.
2. *Chorus doliaris* (Philippi, 1887) 133
   (a, x 1.5; b, x 1.6) USNM 447113; length 18.4 mm, width 13.4 mm.
   Locality: WJZ 266, La Cueva, Chile; Pliocene.
3, 6, 7. *Chorus grandis* (Philippi, 1887) 136
   3. (a, x 1.5; b, x 1.6) USNM 447119; length (18) mm, width 13.4 mm.
      Locality: WJZ 385, Chile, Pliocene.
   6. (x 1) USNM 447074; length 57.6 mm, width 42.0 mm.
      Locality: 87DV 517, Sud-Sacaco, Peru; late Early Pliocene.
   7. (x 1.5) CAS 61701.02; length (30.5) mm, width 22.4 mm.
      Locality: SU 103, Quebrada Culebrón, Coquimbo, Chile; Pliocene.
4. *Chorus giganteus* (Lesson, 1830) 132
   (x 1.5) UCMP D-3735b; length 23 mm, width 14.3 mm.
   Locality: Coquimbo, Chile; Pliocene.
5, 10. *Chorus blainvillei* (d'Orbigny, 1842) 137
   5. (a, x 1.5; b, x 1.6) OSU 37351; length 17.5 mm, width 12 mm.
      Locality: 81DV 273, near Amotape, Peru; Late Pliocene.
   10. (x 0.75) OSU 37357; length 68.9 mm, width 55.3 mm.
      Locality: 81DV 273, near Amotape, Peru; Late Pliocene.
8, 9. *Chorus covacevichi,* n. sp. 136
   8. (x 1.5) USNM 447076 (paratype); length 26.8 mm, width 19.6 mm.
      Locality: WJZ 253, Coquimbo, Chile; Pliocene.
   9. (x 1) USNM 447068 (holotype); length (50.1) mm, width 41.9 mm.
      Locality: WJZ 253, Coquimbo, Chile; Pliocene.

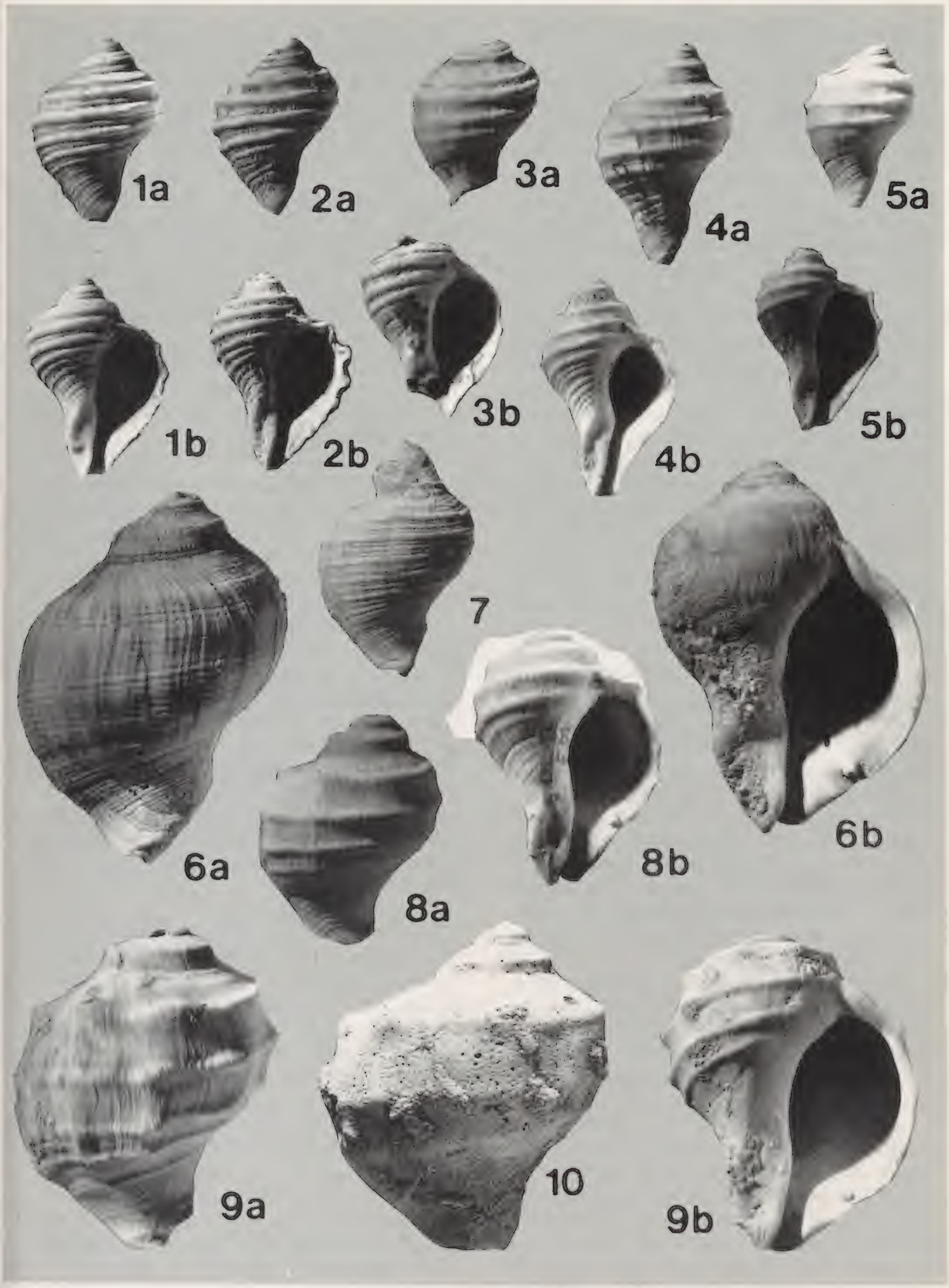

PLATE 2

Description: Length to 90 mm; fusiform; spire 20 percent, neck 35 percent of length; body whorl rounded at shoulder, with no sutural ramp; maximum inflation at or posterior to whorl's midpoint. Axial sculpture of weak opisthocyrt growth lines with apices at the shoulder. Spiral sculpture of juveniles with three, strong, evenly-spaced cords (C2, C3, C4); C2, C3 visible on spire. Third whorl with insertion of weak primary cord (C1) near suture, two weak primary cords (C5, C6) between C4 and nascent spiral groove and strong secondary cords between C1, C2, C3, and C4. Fourth or fifth whorl with subequally strong primary and secondary cords, insertion of single tertiary threads between primary and secondary cords. Adult specimens with subequal secondary cords and tertiary threads; primary cords subdued or absent. Neck with about six spiral cords in juveniles, about nine in adults. Pseudumbilical area and adjacent portion of excavated columella narrow. Posterior portion of inner lip slightly concave to straight; anterior portion straight or turned slightly left. Labral spine shallow infold of outer lip in small juveniles, inset from outer edge of outer lip in adults. Smooth juvenile specimens with weak C1 cord on early whorls, nascent spiral groove, no discernible labral spine, and three weak spiral cords on neck. Larger smooth juveniles with faint tertiary threads, spiral groove, and labral spine. Sculpted juvenile specimens with four strong primary spiral cords (C2, C3, C4, C5), secondary spiral cords between all primary cords.

Type specimen: Holotype, USNM 447116.

Type locality: Quebrada Huaricangana, 40 km west of Nazca, Departamento de Ica, south-central Peru, in bioclastic sandstones on the north flank of Cerro Huaricangana (Text-figure 5); DeVries locality 86DV 528.

Etymology: This species is named in honor of Daniel Frassinetti C., paleontologist with the Museo Nacional de Historia Natural, Santiago, Chile, who has contributed greatly to an understanding of the Tertiary mollusks of Chile.

Occurrence: (Late Miocene) southern Peru to south-central Chile. In the Pisco Basin, radiometric dates of volcanic ashes collected from nearby Aguada de Lomas indicate that the base of the Miocene section, just above which specimens of *Chorus frassinettii* from locality 87DV 531 were taken, is about nine or ten million years old (de Muizon and DeVries, 1985). An unpublished ^{39}Ar-^{40}Ar date of 7.51 ± 0.05 Ma obtained by L. Snee (written communication, 1991) from ash beds underlying coarse-grained *Chorus*-bearing deposits on the south side of Quebrada Huaricangana (sample 87DV 528 1Snee) establishes an age of about eight Ma for *C. frassinettii* specimens from lower in the section (samples 87DV 528-1, 87DV 536-1). An unpublished ^{39}Ar-^{40}Ar date of 6.45 ± 0.03 Ma from an ash bed higher in the same bioclastic sequence (sample 87DV 530a 12Snee) establishes an upper age limit on the age of *C. frassinettii* specimens from Quebrada Huaricangana (sample 87DV 528-3). Higher still in the section, at a level roughly correlative with uppermost Miocene ash beds three km farther east (5.62 ± 0.01 Ma; sample 87DV 532a 1Snee; Snee, written communication, 1990), are beds that overlie the youngest specimens clearly attributable to *C. frassinettii*.

Material examined: All material Late Miocene. USNM 447065, sample 87DV 571-1, El Jahuay, l (47.4) mm, w 34.1 mm; USNM 447066, sample 87DV 571-1, l 19.6 mm, w 14.0 mm; USNM 447067, sample 87DV 571-1, l 37.3 mm, w 27.2 mm; USNM 447082, sample 87DV 536-1, Quebrada Huaricangana, l (48) mm; USNM 447083, Quebrada Huaricangana l (23.4) mm, w 17.9 mm; USNM 447084, sample 87DV 528-3, Quebrada Huaricangana, l 25.5 mm, w 17.2 mm; USNM 447085, sample 87DV 528-3, l 50.5 mm, w (35.4) mm; USNM 447112, sample 87DV 571-1, l 16.0 mm, w 10.6 mm; USNM 447115, sample 86DV 387-3, Quebrada Huaricangana, l (47) mm, w 37.7 mm; 447116, holotype, sample 87DV 528-1, Quebrada Huaricangana, l 83.0 mm, w (56) mm; USNM 447117, locality 87DV 571-1, l 27.3 mm, w 19.1 mm.

Discussion: Juvenile specimens of *C. frassinettii*, n. sp., smooth and strongly sculpted alike, lack the anterior inflation of the body whorl seen in juvenile specimens of *C. grandis*. Those larger juveniles of *C. frassinettii* that are strongly sculpted have primary and secondary spiral cords, which are much stronger and more nearly equal than in any other species of *Chorus*. Adult specimens show the same pattern of subdued primary spiral cords and subequal crinkled secondary cords and tertiary threads as seen in adult specimens of *C. grandis,* but lack a sutural ramp (created by a pronounced inflection at spiral cord C2) and anterior inflation.

Collections made by D. Frassinetti and

V. Covacevich in 1993 from Isla Mocha (about 38°S, central Chile) include large juvenile specimens of *Chorus frassinettii* identical with those from the Pisco Basin and adult specimens that exhibit a range of unusual morphologies, including keeled spiral cords C2, C3, and C4 reminiscent of those seen on some Chilean specimens of *C. doliaris*; elevated spires constituting 30 percent of the shell length; and typically sculpted specimens without any anterior constriction. Pending the acquisition of more specimens from central Chile, including juveniles, the specimens from Isla Mocha will be considered normal and aberrant forms of *C. frassinettii*.

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PLATE 3

Figures Page

1-4. *Chorus frassinettii,* n. sp. 138
1. (x 0.67) USNM 447116 (holotype); length 83.0 mm, width (56) mm.
Locality: 87DV 528-1, Quebrada Huaricangana, Peru; Late Miocene.
2. (x 1) USNM 447065; length (47.4) mm, width 34.1 mm.
Locality: 87DV 571-1, El Jahuay, Peru; Late Miocene.
3. (x 1.5) USNM 447117; length 27.3 mm, width 19.1 mm.
Locality: 87DV 571-1, El Jahuay, Peru; Late Miocene.
4. (x 1) USNM 447067; length 37.3 mm, width 27.2 mm.
Locality: 87DV 571-1, El Jahuay, Peru; Late Miocene.

5,6,7. *Chorus blainvillei* (d'Orbigny, 1842) 137
5. (x 0.75) OSU 37355 (topotype); length 75.8 mm, width 66.8 mm.
6. (x 1) OSU 37353 (topotype); length 45.4 mm, width 33.2 mm.
7. (x 1) OSU 37354 (topotype); length 59.4 mm, width 46.6 mm.
Locality of all: 81DV 272 and 81DV 273, Quebrada Cardo Grande, near Amotape, Peru; late Pliocene.

8. *Chorus grandis* (Philippi, 1887) 136
(x 1) USNM 447078; length 35.6 mm, width 26.5 mm.
Locality: WJZ 385, Chile; Pliocene.

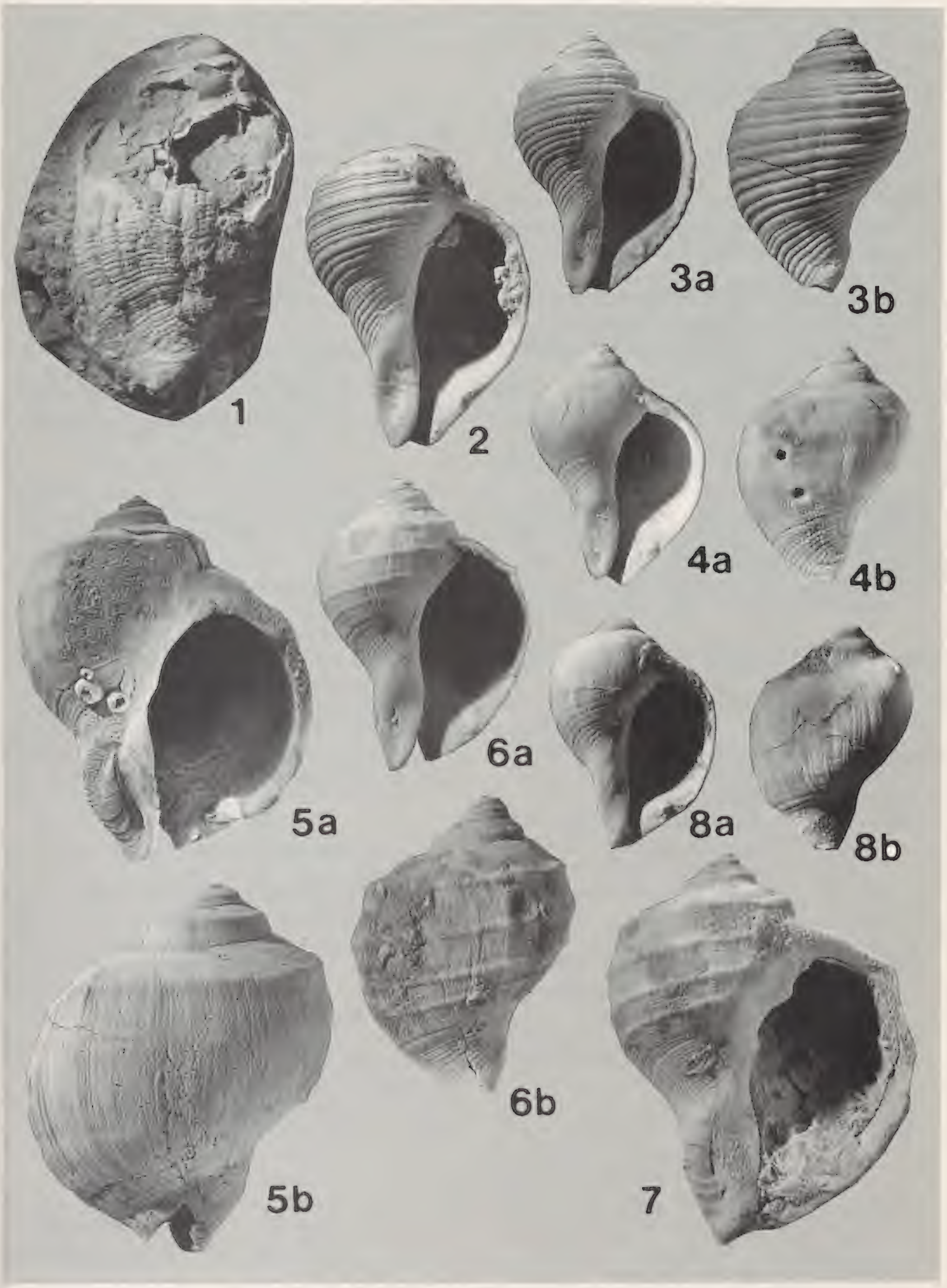

PLATE 3

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VII. LOCALITIES AND SAMPLES

81DV 272 — 2.5 km southwest village of La Brea, Quebrada Songora (DeVries, 1986). Lat. 04°42'49"S, Long. 81°05'35"W (Peru).

81DV 273 — 14 km southeast village of La Brea; northwest arm of Quebrada Cardo Grande (DeVries, 1986). Lat. 04°48'21"S, Long. 81°01'49"W (Peru).

86DV 387-1 — South side Quebrada Huaricangana; in yellow sandstone, fault slice on side of canyon. Lat. 14°58'44"S, Long. 75°19'23"W (Palpa 1:100,000 quadrangle, Peru).

87DV 517-1 — North end of Sud-Sacaco, just below Panamerican Highway, in sandstone. Lat. 15°34'02"S, Long. 74°43'23"W (Acarí 1:100,000 quadrangle, Peru).

87DV 528-1 — South side Quebrada Huaricangana, conglomerates and sandstones descending from flank of Cerro Huaricangana, third gulch from west; 17 m in measured section (unpublished). Lat. 14°57'47"S, Long. 75°16'58"W (Palpa 1:100,000 quadrangle, Peru).

87DV 528-3 — South side Quebrada Huaricangana, conglomerates and sandstones descending from flank of Cerro Huaricangana, east of third gulch from west, along crest of ridge. Lat. 14°57'47"S, Long. 75°16'58"W (Palpa 1: 100,000 quadrangle, Peru).

87DV 530a 12Snee — North side Quebrada Huaricangana, 15-cm thick ash bed, 140.9 m in measured section (unpublished). Lat. 14°55'34"S, Long. 75°15'08"W (Palpa 1: 100,000 quadrangle, Peru).

87DV 532a 1Snee — Quebrada Huaricangana, east of Molde de Queso diatomaceous siltstones, 30-cm thick ash bed, 74.4 m in measured section (unpublished). Lat. 14°55'06"S, Long. 75°15'33"W (Palpa 1: 100,000 quadrangle, Peru).

87DV 536-1 — South side Quebrada Huaricangana, bluff flanking valley, mollusks from lower 25 m of measured section (unpublished). Lat. 14°57'11"S, Long. 75°17'08"W (Palpa 1:100,000 quadrangle, Peru).

87DV 569-1 — West side of Panamerican Highway, across from entrance to Sacaco. southeast-dipping sandstone bed with specimens of *Chorus*. Lat. 15°33'16"S, Long. 74°44'08"W (Yauca 1:100,000 quadrangle, Peru).

87DV 571-1 — El Jahuay, hillside west of Panamerican Highway, south of intersection with road northwest to San Juan de Marcona. (Area disturbed following highway construction in early 1990's.) Lat. 15°26'57"S, Long. 74°52'06"W (Yauca 1:100,000 quadrangle, Peru).

95DV 812-1 — South side of Quebrada Huacllaco, roadcut along Panamerican

Highway. Lat. 15°52'S, Long. 74°11'W (Chala 1:100,000 quadrangle, Peru).

82JM 82024 Río Grande. Lat. 14°55'00"S, Long. 75°07'00"W (Palpa 1:100,000 quadrangle, Peru).

CAS 61701.01 Quebrada Culebrón, Coquimbo, Chile, near bottom of section.

CAS 61701.02 Quebrada Culebrón, Coquimbo, Chile.

CAS 61702.01 Railroad cut 3/4 miles east of Guayacán, Chile.

CAS 61703.01 Upper ten feet of terrace east of Coquimbo, Chile.

RPT 26, 27 Along the Río Acarí, edge of Pampa Totoral, southeast of Sacaco, Peru.

UCMP D-5790 Quebrada Blanca, about 750-1250 m east of Panamerican Highway at Caldera, soft, poorly consolidated, flat-lying beds, with most samples from cliff exposures. [Same as Quebrada Blanca section of Herm (1969, p. 25)]. Lat. 27°03'S, Long. 70°47'W (Caldera 1:50,000 quadrangle, Chile).

UCMP D-5826 Sandy outcrops along bank of stream, 1.5 km south of improved road at Estero El Ganso. Lat. 34°13'S, Long. 71°45'W (Central Rapel 1:50,000 quadrangle, Chile).

UCMP D-3733 Along Panamerican Highway, 10 km north of La Serena, in first deep road cuts north of flat marshland, 1 km northwest junction with side road going northeast to Quebrada Honda; series of thin lenses of fossiliferous sands between beds of gravel. Lat. 29°48'30"S, Long. 71°16'30"W (Coquimbo 1:50,000 quadrangle, Chile).

UCMP D-3735 Along Panamerican Highway, about 11.2 km north of La Serena, from outcrops in deep roadcut along south side of deep quebrada; basal fine-grained sandstones with lenses of gravel. Lat. 29°48'30"S, Long. 71°16'30"W (Coquimbo 1:50,000 quadrangle, Chile).

WJZ 253 Roadcut north of Coquimbo, Chile.

WJZ 266 La Cueva, Chile.

WJZ 281 North shore of Río Tubul, mouth of canyon at southern end of Cerro Rari, near Arauco, Chile. Lat. 37°13'41"S, Long. 73°27'09"W.

WJZ 285 Recent beach, north side of Río Rapel, Chile. Lat. 33°53'36"S, Long. 71°51'W.

WJZ 385 One km east of La Herradura, southwest of village of Miramar. Lat. 29°59'01"S, Long. 71°20'42"W (Coquimbo 1:50,000 quadrangle, Chile).

WJZ 659 Cove on southeast side Punta Middleton, Isla Guamblín, Chile. Lat. 44°51'31"S, Long. 75°09'37"W (Isla Guamblin 1:50,000 quadrangle, Chile).

WJZ 848 Caleta Samuel, Isla Guafo, Chile. Lat. 43°35'32"S.

WJZ 859 Isla Guamblín, Chile.

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A REVIEW OF CYPRAEIFORM GASTROPODS FROM NEOGENE STRATA OF NORTHWESTERN ECUADOR, WITH THE DESCRIPTION OF TWO NEW SPECIES

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MALACOLOGY AND INVERTEBRATE PALEONTOLOGY SECTIONS
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I. ABSTRACT

Six cypraeacean species, two of them new, and one unidentified triviid specimen are reviewed from Neogene strata of northwestern Ecuador. New species of *Zonaria* s.s. and *Z. (Pseudozonaria)* are described from the lower Pliocene Esmeraldas beds of the Onzole Formation. These new species and *Jenneria (Jenneria) panamensis* (Olsson, 1967) are the first cypraeaceans reported from the Esmeraldas beds. The unidentified triviid is the first of its kind reported from the Neogene of Ecuador. Three previously described cypraeid species are also included in this review.

II. INTRODUCTION

Cypraeid, ovulid, and triviid gastropods are rare in the Neogene rock record of northwestern Ecuador. Herein are the first reports of these groups from the lower Pliocene Esmeraldas beds of the Onzole Formation and a review of the species from the upper Miocene Angostura and Guayacan formations and the lower Pliocene Jama Formation. All six of the species included here are extinct; however, all of the genera and/or subgenera are represented in the living fauna of either the tropical eastern Pacific Ocean or the Caribbean Sea.

Pilsbry and Olsson (1941) described *Cypraea cayapa* from the lower Pliocene Jama Formation, the first reported Neogene cypraeid from Ecuador. Marks (1951) identified poorly preserved single specimens from the "Blue siltstone" member of the upper Miocene Daule Formation [= Guayacan Formation] as *Cypraea* cf. *C. henekeni* and *Cypraea* sp. Unfortunately, these specimens are unavailable for examination. In 1964, Olsson described *Cypraea (Pseudozonaria) telembiensis* from the upper Miocene Angostura Formation near Telembi, Río Cayapas. From the same formation he reported two poorly preserved specimens of *Siphocypraea (Muracypraea) henekeni* from Cueva de Angostura, Río Santiago. Most recently Olsson (1967) described *Jenneria panamensis* from the upper Pliocene Charco Azul Formation, Río Blanco, Chiriquí Province, Panamá and it is herein reported from the Esmeraldas beds of the Onzole Formation at Quebrada Camarones. Two new species, *Zonaria (Zonaria) pittorum* and *Z. (Pseudozonaria) cathyae*, are the first cypraeids described from the Esmeraldas beds of the Onzole Formation (Text-figure 1). An incomplete specimen of *Pusula (Pusula)* sp. from these same beds is the first reported fossil triviid from Ecuador.

III. STRATIGRAPHIC NOMENCLATURE AND AGE

Because much has been published recently concerning the age of the Neogene formations of northwestern Ecuador (Haman and Kohl, 1986; Hasson and Fischer, 1986; DuShane, 1988; Vokes, 1988; 1989; 1990; Whittaker, 1988; Pitt and Pitt, 1989; 1992; 1997), only a brief overview of stratigraphic nomenclature and age will be discussed.

Miocene Units

The upper Miocene Angostura Formation of Stainforth (1948:142), named for outcrops along the Río Santiago, Esmeraldas Province, is the Ecuadorian equivalent of the Gatun Formation of Panamá (Pitt and Pitt, 1992). However,

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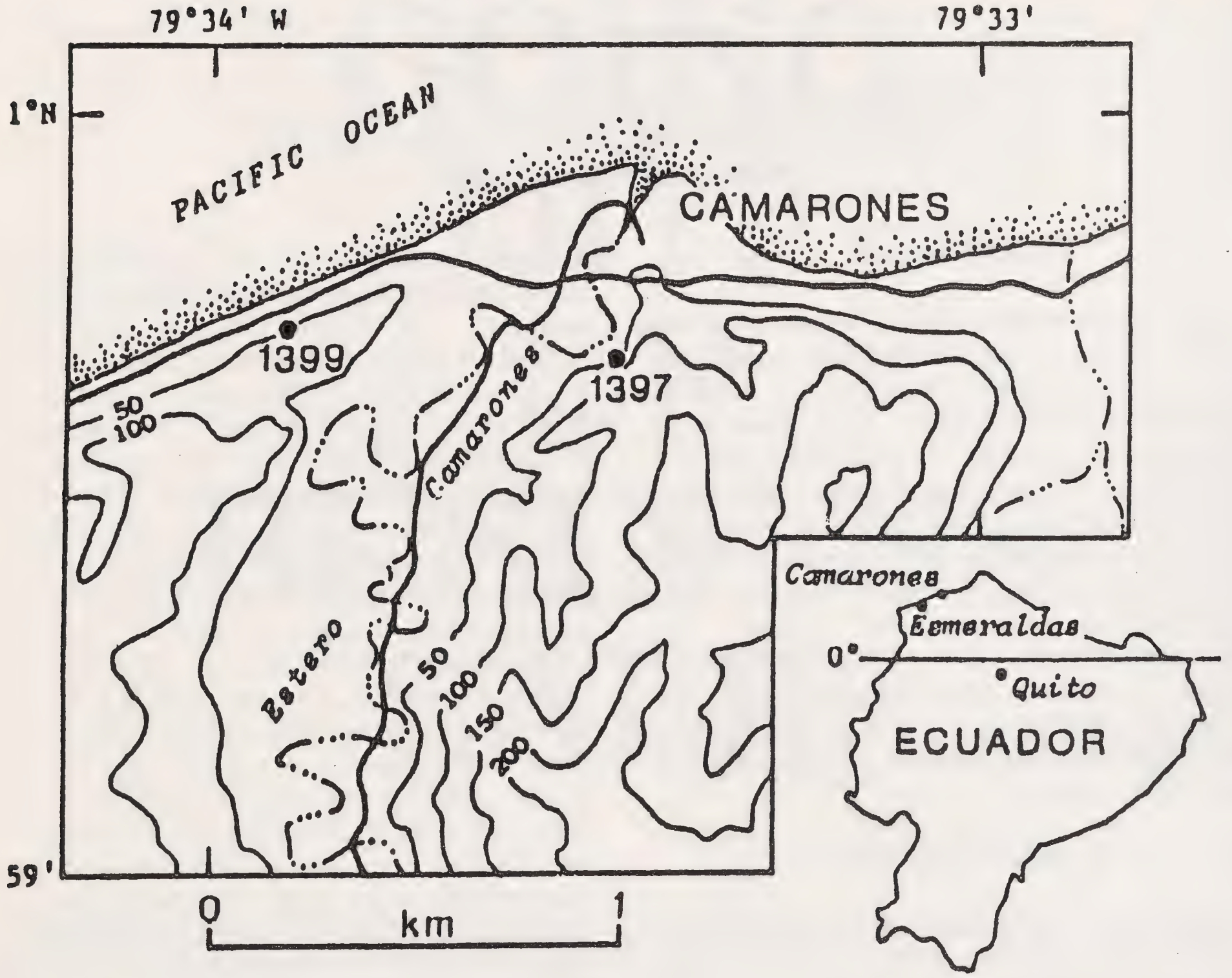

Text-figure 1. Index map of northwestern Ecuador showing type localities (TU 1397 and 1399 [=LACMIP localities 16944 and 16822 respectively]) of new species described herein [modified from DuShane, 1988]. Contour interval 50 m.

the uppermost part of the Gatun Formation may be of lower Pliocene age (Vokes, 1990). Olsson (1964:8) stated that this formation "is largely barren, but at a few places there are lenses or interbeds filled with finely preserved fossils." He also noted a close faunal relationship between the Angostura and Gatun formations.

Whittaker (1988) formally proposed the term Guayacan Formation [= the Blue Siltstone Member of the Daule Formation of Marks (1951)] for widespread upper Miocene strata in the Manabí Basin, as Mark's terminology did not conform to international guidelines for the naming of lithostratigraphic units (Hedberg, 1976). Additionally, the formational names of Bristow's (1976) Daule Group, which were derived from the Borbón Basin, were replaced by Whittaker's (1988) terminology based on Manabí Basin strata. The age of the Guayacan Formation is based on age-diagnostic planktic foraminifera.

Pliocene Units

Olsson (1942) proposed the name "Esmeraldas formation" for "the highly foraminiferal, tuffaceous shales so extensively exposed along the coast of Esmeraldas and along the Esmeraldas River itself" and thought it equivalent to the Borbón Formation. However, the Esmeraldas Formation is, in fact, correlative to the Onzole Formation of Stainforth (1948) (Pitt and Pitt, 1989). Bristow (1976) stated that the Esmeraldas Formation was improperly defined by Olsson (1942) and that the name Onzole Formation should be retained. Vokes (1988) suggested usage of "Esmeraldas beds" for "the mollusk-rich, shallow water

gravity flows" in the upper part of the Onzole Formation. This usage is retained herein. Haman and Kohl (1986) based the age of strata at Quebrada Camarones (= Esmeraldas beds of the Onzole Formation) on the presence of the benthic foraminiferal genus *Montfortella.* Micropaleontologic anaylses by Hasson and Fischer (1986) yielded a lower Pliocene (= Zanclian Stage of Seguenza, 1868) age for the Esmeraldas beds. Whittaker (1988) cited the age of the Onzole Formation as between upper Miocene and early Pliocene but considered the upper part of the Onzole, presumably including the Esmeraldas beds, to be entirely Pliocene as dated by benthic foraminifera.

Based upon a rich molluscan fauna, the lower Pliocene Jama Formation was proposed by Pilsbry and Olsson (1941) for exposures along Bahía Jama, Manabí Province. Benthic foraminifera within the formation indicate littoral to sublittoral depositional environments. Whittaker (1988) equated the Jama Formation with his lower Pliocene Bahía Formation [= Upper Calcareous member of Marks (1951)], both within the Manabí Basin, and he separated them on lithologic and faunal differences.

IV. ACKNOWLEDGMENTS

William D. and Lois J. Pitt, Sacramento, California, kindly donated personally collected specimens, provided stratigraphic and paleontologic information about the Onzole and Angostura formations, and reviewed an early version of the manuscript. Emily H. Vokes (TU), Elana Benamy and Gary Rosenberg (ANSP), Jean F. DeMouthe, Elizabeth Kools, and the late Tony Summers (CAS), Paul Jeffrey (BMNH), David R. Lindberg, Christopher P. Meyer, and Karen Wetmore-Grycewicz (UCMP), and Warren H. Blow, Jann Thompson, and Thomas R. Waller (USNM) granted numerous requests for specimen loans and locality information from their respective institutions. Librarians Donald W. McNamee and Mark Herbert (LACM Research Library) and Suzanne Henderson, Jean Crampon, and Melinda Hayes (Alan Hancock Foundation, University of Southern California) processed numerous interlibrary loan requests and aided in locating rare and obscure references. James H. McLean (Natural History Museum of Los Angeles County, Malacology) and Richard L. Squires (California State University, Northridge) reviewed the manuscript and offered helpful criticisms.

ABBREVIATIONS CITED

ANSP:	Academy of Natural Sciences of Philadelphia
BM(NH):	The Natural History Museum, London
CAS:	California Academy of Sciences, San Francisco
LACMIP:	Natural History Museum of Los Angeles County (Invertebrate Paleontology Section)
P:	Collecting locality numbers of W.D. and L.J. Pitt
TU:	Tulane University, New Orleans
UCMP:	University of California, Museum of Paleontology, Berkeley
USNM:	National Museum of Natural History, Smithsonian Institution, Washington, D.C.

V. SYSTEMATICS

For the most part, the classification scheme of Schilder and Schilder (1971) is utilized for generic and higher level taxonomy. The notable exception is that the *Siphocypraea (Muracypraea)* group is accepted as a full genus, as proposed by Kay (1995). Synonymy citations are limited to original descriptions, material examined, and all records of each species from Ecuador. Measurement parameters are defined as follows: length = greatest distance between anterior and posterior ends; width = greatest distance between lateral margins; and height = greatest distance between base and dorsum.

Superfamily VELUTINACEA Gray, 1840
Family TRIVIIDAE Troschel, 1863
Subfamily TRIVIINAE Troschel, 1863
Tribe PUSULINI Schilder, 1936

Genus PUSULA Jousseaume, 1884

Pusula JOUSSEAUME, 1884, Bull. Soc. Zool. France, v. 9, p. 99.

Type Species: *Cypraea radians* Lamarck, 1810, by original designation; Recent, Panamic Province.

Subgenus PUSULA Jousseaume, 1884

PUSULA (PUSULA) sp.

Plate 1, figure 1

Occurrence: Lower Pliocene Esmeraldas beds, Onzole Formation.

Figured Specimen: LACMIP hypotype 12429, TU locality 1399 (= locality P-101; LACMIP locality 16882), 16.8 mm length, 11.7 mm width, 10.4 mm height, H.E. and E.H. Vokes collectors (pl. 1, fig. 1).

Discussion: Only a single incomplete specimen of *Pusula (Pusula)* sp. is known from the Esmeraldas beds of the Onzole Formation. This fragment most closely resembles the Recent Panamic species *P. (P.) radians* (Lamarck, 1810) but has more numerous, finer ribs. This is the first published report of a fossil triviid from the Neogene of Ecuador.

Superfamily CYPRAEACEA Rafinesque, 1815

Family CYPRAEIDAE Rafinesque, 1815

Subfamily BERNAYINAE Schilder, 1927

Tribe BERNAYINI Schilder, 1927

Genus MURACYPRAEA Woodring, 1957

Muracypraea WOODRING, 1957, The Nautilus, v. 70, p. 89 (subgenus of *Cypraea*).

Type Species: *Cypraea mus* Linnaeus, 1758, by original designation; Recent, Panamá, Colombia, and Venezuela.

MURACYPRAEA CAYAPA (Pilsbry and Olsson, 1941)

PLATE 1

Figures Page

1. *Pusula (Pusula)* sp. 150
LACMIP 12429 (hypotype); 16.8 mm length, 11.7 mm width, 10.4 mm height (x2.3).
Locality: TU 1399 (= P-101; LACMIP 16882), Esmeraldas beds, Onzole Formation, Ecuador.

2,3. *Muracypraea cayapa* (Pilsbry and Olsson, 1941) 150
ANSP 13665 (holotype); 64.3 mm length, 52.7 mm width, 42.4 mm height (x0.62).
Jama Formation, Ecuador.

4-6. *Muracypraea "henekeni"* (Sowerby, 1850) 152
4. LACMIP 12430 (hypotype); 50.5 mm length, 21.9 mm width, 31.2 mm height (x0.94).
Locality: TU 1507 (= P-102; LACMIP 16943), Angostura Formation, Ecuador.
5,6. ACMIP 12431 (hypotype); 42.1 mm length, 34.4 mm width, 23.2 mm height (x0.95).
Locality: TU 1507 (= P-102; LACMIP 16943), Angostura Formation, Ecuador.

7,8. *Zonaria (Zonaria) pittorum* Groves, n.sp 153
LACMIP 12432 (holotype); 40.1 mm length, 27.3 mm width, 20.9 mm height (x1.0).
Locality: TU 1399 (= P-101; LACMIP 16882), Esmeraldas beds, Onzole Formation, Ecuador.

9,10. *Zonaria (Pseudozonaria) cathyae* Groves, n.sp. 154
LACMIP 12433 (holotype); 22.3 mm length, 15.8 mm width, 12.8 mm height (x1.8).
Locality: TU 1397 (= P-100; LACMIP 16944), Esmeraldas beds, Onzole Formation, Ecuador.

11,12. *Zonaria (Pseudozonaria) telembiensis* (Olsson, 1964) 154
USNM 644048 (holotype); 19.5 mm length, 13.4 mm width, 10.1 mm height (x1.9)
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13,14. *Jenneria (Jenneria) panamensis* (Olsson, 1967) 155
LACMIP 12434 (hypotype); 25.8 mm length, 16.9 mm width, 11.8 mm height (x1.5)
Locality: TU 1397 (= P-101; LACMIP 16944), Esmeraldas beds, Onzole Formation, Ecuador.

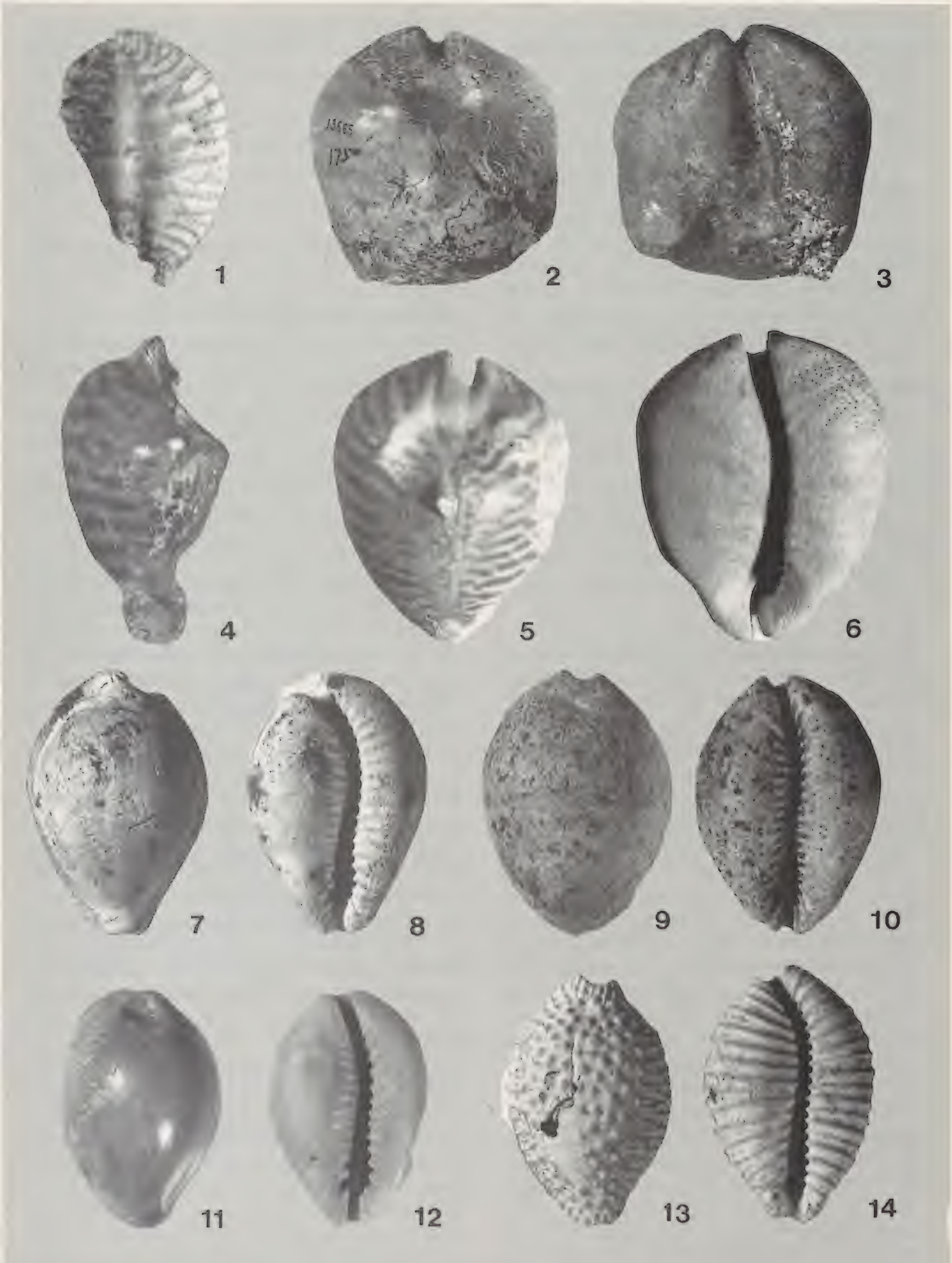

PLATE 1

Plate 1, figures 2, 3

Cypraea cayapa PILSBRY and OLSSON, 1941, Proc. Acad. Nat. Sci. Philadelphia, v. 93, p. 41-42, pl. 7, fig. 4; INGRAM, 1947, Bulls. Amer. Paleontology, v. 31, no. 120, p. 60-61, 89-90; INGRAM, 1947, Bulls. Amer. Paleontology, v. 31, no. 122, p. 145; WOODRING, 1959, U.S. Geol. Surv. Prof. Paper 306-B, p. 194; RICHARDS, 1968, Spec. Pub. Acad. Nat. Sci. Philadelphia, v. 8, p. 113.

Siphocypraea cayapa (Pilsbry and Olsson). SCHILDER, 1961, Arch. Moll., v. 90, no. 4/6, p. 148; PETUCH, 1979, Bull. Mar. Sci., v. 29, no. 2, p. 217; PETUCH, 1988, Neogene Hist. Trop. Amer. Moll., p. 100.

Siphocypraea (Muracypraea) cayapa (Pilsbry and Olsson). SCHILDER and SCHILDER, 1971, Inst. Roy. Sci. Nat. Belgique, Mem. 85, p. 29, 104.

Barycypraea (Muracypraëa) cayapa (Pilsbry and Olsson). GROVES, 1993, West. Soc. Malac., Ann. Rept., v. 25, p. 12.

Muracypraea cayapa (Pilsbry and Olsson). GROVES, 1997, West. Soc. Malac., Ann. Rept., v. 29, p. 8.

Type Material: Holotype ANSP 13665; 64.3 mm length (incomplete), 51.7 mm width, 42.4 mm height, A.A. Olsson collector (pl. 1, figs. 2, 3).

Type Locality: Puerto Jama, Manabí Province, Ecuador; lower Pliocene, Jama Formation.

Occurrence: Known only from a single incomplete specimen from the type locality (Pilsbry and Olsson, 1941).

Discussion: Although approximately one-third of the anterior of this large specimen is missing, it unlikely to be confused with any other cypraeid species from Ecuador. Similar large *Muracypraea* specimens from Venezuela, Baja California Sur, Mexico, and Imperial County, California, were compared to *M. cayapa* and together might represent a separate lineage based on their shared prominent pair of posterior dorsal tubercules, highly angular shape, and highly arched dorsum.

MURACYPRAEA "HENEKENI"
(Sowerby, 1850)
Plate 1, figures 4, 5, and 6

Cypraea henikeri SOWERBY, 1850, Geol. Soc. London, Quart. Jour., v. 6, p. 45, pl. 9, fig. 3 [error for *henekeni*].

Cypraea cf. *C. henekeni* Sowerby. MARKS, 1951, Bulls. Amer. Paleontology, v. 33, no. 139, p. 376.

Siphocypraea (Muracypraea) henekeni (Sowerby). OLSSON, 1964, Neogene Moll. Northwest. Ecuador, p. 176-177, pl. 31, figs. 3-3a.

Type Material: Lectotype (designated by Pflug, 1961:21) BM(NH) G83940; paralectotypes, here recognized, BM(NH) GG20023, GG20024, GG20025, GG20026 and GG20027.

Type Locality: Río Yaque, northern Dominican Republic (Woodring, 1959); late Miocene, presumably Cercado or Gurabo Formation.

Occurrence: PANAMÁ: Gatun Formation (Woodring, 1959; Pit and Pitt, 1993); ECUADOR: Angostura Formation (Olsson, 1964); Blue Siltstone Member, Daule Formation [= Guayacan Formation] (Marks, 1951); COLOMBIA: Nariño Department (herein).

Figured Specimens: LACMIP 12430, TU locality 1507 (= P-102; LACMIP locality 16943), 50.5 mm length, 21.9 mm width, 31.2 mm height [incomplete] (pl. 1, fig. 4), H.E. and E.H. Vokes collectors; LACMIP 12431, TU locality 1507 (= LACMIP locality 16945), 42.1 mm length, 34.4 mm width, 23.2 mm height (pl. 1, figs. 5, 6), H.E. and E.H. Vokes collectors.

Material Examined: ECUADOR: 1 partial specimen, locality P-102, Angostura Formation, Punta Verde, Esmeraldas Province (Coll. W.D. and L.J. Pitt); 1 specimen, TU locality 1507, Angostura Formation, Río Verde, Esmeraldas Province (Coll. H.E. and E.H. Vokes); 1 specimen, USNM 644046, Angostura Formation, Río Santiago, Esmeraldas Province; and 1 specimen, USNM 644047, Angostura Formation, Río Santiago, Esmeraldas Province; PANAMÁ: 1 specimen, locality P-95, Gatun Formation, Cativa, Colón Province (Coll. W.D. and L.J. Pitt); 1 specimen, ANSP 315087, Gatun Formation, Cativa, Colón Province (Coll. W.C. Gruff); 3 specimens, TU locality 1432, Gatun Formation, Cativa, Colón Province (Coll. H.E. and E.H. Vokes); 2 specimens, TU locality 960 [= locality 139E of Woodring (1959)], Gatun Formation, Isla Payardi, Colón Province (Coll. H.E. and E.H. Vokes); 5 specimens, TU locality 958, Gatun Formation, east of Cativa, Colón Province (Coll. H.E. and E.H. Vokes); 5 specimens, TU locality 757, Gatun Formation, east of Cativa, Colón Province (Coll. H.E. and E.H. Vokes); 1 specimen, TU locality 1433, Gatun

Formation (Coll. H.E. and E.H. Vokes); 1 specimen, LACMIP locality 16936, Gatun Formation (Coll. T. Bratcher); and COLOMBIA: 1 partial specimen, UCMP locality C-14311, Nariño Department (Coll. Tropical Oil Company).

Two of Woodring's (1959) hypotypes [USNM 562581 and 562582] from the Gatun Formation of Panamá and a single specimen from the San Ignacio area, Baja California Sur, Mexico [USNM collection], may also represent *M. "henekeni."*

Discussion: Numerous forms and/or varieties identified as *M. henekeni* were synonymized by Woodring (1959). However, specimens from Panamá and Ecuador (and a single partial specimen from southwestern Colombia) differ significantly enough to justify splitting from the nominal species. They are generally smaller, have a distinct triangular or arrowhead shape, possess prominent pairs of dorsal tubercules, and in some instances have a central "spike-like" dorsal tubercule. Many of the specimens also display original color striping and blotching of dull reddish brown and yellowish orange uncommonly found in the nominal species. Woodring (1959) acknowledged the variability of *M. henekeni* and the excess of names applied to this species, and he stated that "some of the names in the synonymy may prove to be useful for local populations when adequate samples are available." Groves and Arnold (in preparation) will provide further justification in splitting the western Caribbean and Ecuadorian specimens from *M. henekeni* of the Dominican Republic, Trinidad, Venezuela, and northern Colombia. Specimens herein therefore are referred to *M. "henekeni"* in the interim. Pilsbry and Olsson (1941:42) mentioned that "a smaller, undescribed species occurs in the Miocene of the Río Santiago, northern Ecuador, but none are known in the present west coast fauna." This form might represent *M. "henekeni"* of this present study, however, their whereabouts are unknown.

Subfamily ERRONEINAE Schilder, 1927
Tribe ZONARIINI Schilder, 1932
Genus ZONARIA Jousseaume, 1884

Zonaria JOUSSEAUME 1884, Bull. Soc. Zool. France, v. 9, p. 92-93.

Type Species: *Cypraea zonata* Lamarck, 1810 (not Chemnitz, 1788) [= *Cypraea zonaria* Gmelin, 1791], by original designation; Recent, West Africa.

Subgenus ZONARIA Jousseaume, 1884

ZONARIA (ZONARIA) PITTORUM Groves, n.sp.
Plate 1, figures 7, 8

Zonaria (Zonaria) n.sp. GROVES, 1997, West. Soc. Malac., Ann. Rept., v. 29, p. 8.

Diagnosis: A *Zonaria* s.s. with lengthened anterior, weak teeth on anterior canal, and smooth narrow fossula.

Description: Shell shape pyriform, medium in size; spire covered; dorsum prominently arched; maximum height slightly posterior of midpoint; aperture slightly curved posteriorly toward columella; denticulation strong with smooth interstices; labial lip with 19 teeth; columellar lip with 17 teeth; strong anterior canal teeth, weak posterior canal teeth; fossula smooth and narrow; basal marginal callus moderate to prominent; deep and well developed terminal canals.

Type Material: Holotype LACMIP 12432; length 40.1 mm, width 27.3 mm, height 20.9 mm, H.E. and E.H. Vokes collectors (pl. 1, figs. 7, 8).

Type Locality: TU locality 1399 (= P-101; LACMIP locality 16882), lower Pliocene Esmeraldas beds, Onzole Formation; roadcut on west side of village of Camarones, 20 km east of bridge over Río Esmeraldas, Esmeraldas Province, Ecuador.

Occurrence: Esmeraldas beds, Onzole Formation, Ecuador; TU locality 1399 [= P-101; LACMIP locality 16882] (1 specimen).

Discussion: The new species is most similar to *Zonaria (Zonaria) porcellus cocconii* (Mayer, 1875) from the middle to upper Pliocene (= Piacenzian Stage of Mayer-Eymar, 1857) rocks of northern Italy. *Zonaria (Z.) pittorum*, n.sp., has a more sinuous aperture and fewer, stronger apertural teeth that extend further onto the labial and columellar surfaces than in *Z. (Z.) porcellus cocconii.* Both species differ from *Z. (Z.) porcellus* (Brocchi, 1814), also from the middle to upper Pliocene rocks of northern Italy, by having a more inflated columella, a higher arched dor-

sum, and a more prominent basal marginal callus. Inzani (1995) figured specimens that display a range of minor shell differences, but all are consistent with the subspecies *Z. (Z.) porcellus cocconii.*

Etymology: This new species is named for William D. and Lois J. Pitt, Sacramento, California, in recognition of their numerous important paleontological works on the Tertiary of Ecuador and Panamá.

Subgenus PSEUDOZONAIRA Schilder, 1927

Pseudozonaria SCHILDER, 1927, Arch. Naturges., v. 91A, p. 115.

Type Species: *Cypraea arabicula* Lamarck, 1810, by original designation; Recent, Panamic Province.

ZONARIA (PSEUDOZONARIA) CATHYAE Groves, n.sp.

Plate 1, figures 9, 10

Zonaria (Pseudozonaria) n.sp. GROVES, 1997, West. Soc. Malac., Ann. Rept., v. 29, p. 8.

Diagnosis: A *Zonaria (Pseudozonaria)* with oval shape, strong teeth on terminal canals, and wide, denticulated fossula.

Description: Shell oval in shape, medium in size; spire covered, with prominent pit near spire callus; dorsum highly arched, maximum height slightly posterior of midpoint; wide straight aperture slightly curved posteriorly toward columella; denticulation fine and incised with smooth interstices; labial lip with 18 teeth; columellar lip with 16 teeth; strong teeth on terminal canals; wide fossula crossed by columellar teeth; basal marginal callus prominent; deep and well developed terminal canals.

Type Material: Holotype LACMIP 12433; length 22.3 mm, width 15.8 mm, height 12.8 mm, H.E. and E.H. Vokes collectors (pl. 1, figs. 9, 10).

Type Locality: TU locality 1397 (= P-100; LACMIP locality 16944), lower Pliocene Esmeraldas beds, Onzole Formation; Quebrada Camarones, cut-bank on east side of canyon, east of the village of Camarones, 20 km east of bridge over Río Esmeraldas, Esmeraldas, Esmeraldas Province, Ecuador.

Occurrence: Esmeraldas beds, Onzole Formation; TU locality 1397 [= P-100; LACMIP locality 16944] (1 specimen).

Discussion: The new species is most similar to *Z. (P.) portelli* (Petuch, 1990) from the Pleistocene Bermont Formation, Dade County, Florida and the Recent Panamic *Z. (P.) robertsi* (Hidalgo, 1906). *Zonaria (Pseudozonaria) cathyae*, n.sp., has finer and more numerous apertural teeth than both similar species, a more prominent basal marginal callus, and a thicker more prominent labial lip with incised teeth. The upper Miocene *Zonaria (Pseudozonaria) telembiensis* differs from *Z. (P.) cathyae* by its smaller size, fewer and coarser apertural teeth, and a weaker basal marginal callus.

Etymology: This new species is named for my wife Cathy L. Groves, of the Echinoderms Section of Invertebrate Zoology, Natural History Museum of Los Angeles County.

ZONARIA (PSEUDOZONARIA) TELEMBIENSIS (Olsson, 1964)

Plate 1, figures 11, 12

Cypraea (Pseudozonaria) telembiensis OLSSON, 1964, Neogene Moll. Northwest. Ecuador, p. 175, pl. 31, figs. 6a-b.

Zonaria (Pseudozonaria) telembiensis (Olsson). SCHILDER and SCHILDER, 1971, Inst. Roy. Sci. Nat. Belgique, Mem. 85, p. 46, 162; GROVES, 1993, West. Soc. Malac., Ann. Rept., v. 25, p. 12; GROVES, 1997, West. Soc. Malac., Ann. Rept., v. 29, p. 8.

Type Material: Holotype USNM 644048, 19.5 mm length, 13.4 mm width, 10.1 mm height, A.A. Olsson collector (pl. 1, figs. 11, 12).

Type Locality: Río Cayapas, Telembi, Esmeraldas Province, Ecuador; upper Miocene, Angostura Formation.

Occurrence: Known only from a single specimen from the type locality (Olsson, 1964).

Discussion: Zonaria (Pseudozonaria) telembiensis is the earliest known species of its subgenus.

Family OVULIDAE Fleming, 1822
Subfamily EOCYPRAEINAE Schilder, 1924
Tribe CYPROGLOBININI Schilder, 1924
Genus JENNERIA Jousseaume, 1884

Jenneria JOUSSEAUME, 1884, Bull. Soc. Zool. France, v. 9, p. 98-99.

Type Species: *Cypraea pustulata* [Lightfoot, 1786], by original designation; Recent, Panamic Province.

Subgenus JENNERIA Jousseaume, 1884

JENNERIA (JENNERIA) PANAMENSIS (Olsson, 1967) Plate 1, figures 13, 14

Cypropterina pustulata (Lamarck, 1810). OLSSON, 1942, Bulls. Amer. Paleontology, v. 27, no. 106, p. 21. Not *Cypraea pustulata* [Lightfoot, 1786].

Jenneria panamensis OLSSON, 1967, Notulae Naturae, p. 9, pl. 1, figs. 3-3a.

Cypropterina (Jenneria) panamensis (Olsson). SCHILDER and SCHILDER, 1971, Inst. Roy. Sci. Nat. Belgique, Mem. 85, p. 71, 141; GROVES, 1993, West. Soc. Malac., Ann. Rept., v. 25, p. 12; GROVES, 1997, West. Soc. Malac., Ann. Rept., v. 29, p. 8.

Type Material: Holotype NSP 31312, missing (E. Benamy, pers. commun., 1990).

Type Locality: Upper Pliocene, Charco Azul Formation, Río Blanco, Burica Peninsula, Chiriquí Province, Panamá (Olsson, 1967).

Figured Specimen: LACMIP 12434, TU locality 1399 (= P-101; LACMIP locality 16882); length 25.8 mm, width 16.9 mm, height 11.8 mm, H.E. and E.H. Vokes collectors; roadcut on west side of village of Camarones, 20 km east of bridge over Río Esmeraldas, Esmeraldas, Esmeraldas Province, Ecuador.

Occurrence: Charco Azul Formation, Panamá (Olsson, 1967); Esmeraldas beds, Onzole Formation, Ecuador (herein).

Discussion: Jenneria (Jenneria) panamensis is the only species of fossil ovulid from the Neogene of Ecuador. The Pleistocene through Recent Panamic species *J. (J.) pustulata* [Lightfoot, 1786] appears to be more closely related to the "Florida group" of pustularias of Olsson (1967), based on shell characteristics than to *J. (J.) panamensis* and is the sole surviving species of this genus.

VI. LOCALITY REGISTER OF FIGURED SPECIMENS

ANSP 13665. Jama Formation, Puerto Jama, Manabí Province, Ecuador. Early Pliocene.

TU 1397. Esmeraldas beds, Onzole Formation, Quebrada Camarones, cutbank on east side of canyon, which is at east edge of village of Camarones, 20 km (by road) east of bridge over Río Esmeraldas, Esmeraldas Province, Ecuador. Early Pliocene. [= P-100; LACMIP 16944].

TU 1399. Esmeraldas beds, Onzole Formation, road-cut on west side of village of Camarones, which is 20 km (by road) east of bridge over Río Esmeraldas, Esmeraldas Province, Ecuador. Early Pliocene. [= P-101; LACMIP 16882]

TU 1507. Angostura Formation, large point just east of Río Verde, or approximately 30 km east of Río Esmeraldas, Esmeraldas Province, Ecuador. Late Miocene. [= P-102; LACMIP 16943].

USNM 644048. Angostura Formation, Telembi, Río Cayapas, Manabí Province, Ecuador. Late Miocene.

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THE TULANE GEOLOGICAL COLLECTIONS

In 1956 when Harold E. Vokes came to Tulane University to build up the Geology Department and institute a graduate program in Geology and Paleontology, the collections of fossil and Recent material consisted of the remnants of what originally had been exhibited at the Louisiana Cotton Centennial Exposition. This exposition, which marked the 100-year anniversary of the shipment of the first bale of cotton from the port of New Orleans, was held in what is now Audubon Park, across St. Charles Avenue from the present Tulane campus. Like all such expositions at this time, fossils, minerals, zoological specimens, etc., were sent by countries all over the world (there was a beautiful mineral collection from Uruguay, for example). After the exposition ended the material was donated to Tulane University and for the next 70 years comprised a "natural history museum" in the attic of the main administration building, Gibson Hall. However, in 1956, coinciding with Vokes's arrival, the University disbanded the museum and distributed the specimens between the Geology and Biology departments.

In this collection there were beautiful European ammonites and such, but almost no American fossils. Professor Vokes's first order of priority was to establish a collection of stratigraphic guide fossils for the purposes of teaching Stratigraphic Paleontology. To this end, 49 of the first 50 TU fossil localities are Paleozoic.

But soon Professor and Mrs. Vokes turned to the Cenozoic outcrops of the Gulf and Atlantic Coastal Plain, and in 1962 drove from New Orleans to Isla Mujares, Quintana Roo, Mexico, beginning their fascination with the Tertiary formations of the Isthmus of Tehuantepec. In 1968 a longer drive from New Orleans to Panama introduced them to the beautiful outcrops in Panama and Costa Rica, which were subsequently revisited many times. In 1976 political stability finally permitted collecting in the Dominican Republic and for the next eight years this was the scene of greatest interest.

Other trips added localities in France, Australia, New Zealand, South America, and other sites throughout the world. By 1995, when Mr. Vokes's health ended their activites, the Tulane collection numbered 1545 localities, that last number being, of all places, a hitherto undiscovered locality on the Chipola River, in an area where they already had 55 localities.

At the same time the fossils were being collected, Recent mollusks were also being added to the collections, with a total of 666 localities ranging from Iceland to Antarctica, although the vast majority were more tropical in nature -- especially from the Yucatan Peninsula, as a result of the Vokes's publication on the fauna of that area.

But in 1996 Emily Vokes retired from Tulane, Harold having already been required to retire at the then mandatory age of 70 in 1978. With the realization that no one at the Tulane Geology Department any longer had any interest in these collections it was agreed that the material be placed in institutions where it would be conserved (hopefully) in perpetuity. Therefore, the collections have been dispersed to three institutions. All of the Dominican Republic material, as well as the Paleozoic and most of the Mesozoic localities are now at the Paleontological Research Institution, Ithaca, New York. The rest of the non-U.S. Tertiary, as well as a few Mesozoic localities, are now at the U.S. National Museum of Natural History, Washington, D.C. But the bulk of the collection, including almost all of the U.S. Cenozoic localities, as well as all of the Recent mollusks (except for Australia and New Zealand localities, which were given to the USNM) are now in the Florida Museum of Natural History, Gainesville, Florida.

DISTRIBUTION AND PALEOECOLOGY OF *GLOTTIDIA INEXPECTANS* OLSSON, 1914 (BRACHIOPODA: LINGULIDAE)

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I. ABSTRACT

The lingulid brachiopod *Glottidia inexpectans*, previously known from the Yorktown Formation in Virginia, is here reported from the Early Pliocene beds of South Carolina and Florida. *Glottidia inexpectans* differs from intertidal to shallow subtidal Recent species in apparent habitat bathymetry. In Virginia, the associated molluscs indicate water depths of 40 to 60 meters, the fishes somewhat deeper. Associated taxa in Florida apparently lived in subtidal habitats to 20 meters.

The proclivity of *G. inexpectans* for shell degradation parallels the taphonomic destruction patterns of the more thoroughly studied Recent species. Preservation of specimens in any numbers must combine structural integrity with protection from chemical deterioration. The 155 pairs of juvenile *G. inexpectans* here reported from Carter's Grove, Zone 1, Yorktown Formation, and the smaller population reported by Olsson (1914) were preserved within closed valves of *Chesapecten jeffersonius,* a large species of scallop with thick, well-inflated valves. These two populations probably represent single spatfalls of *Glottidia* larvae which settled in gaping scallop shells partially filled with sediment. They then died of starvation or oxygen deprivation after the valves closed by relaxation of the ligament or by burial. The physical protection afforded by this micro-habitat appears essential for preservation of fragile subadult shells. Interpreting this assemblage prompted a review of the systematics, ecology, distribution, and taphonomy of *Glottidia.*

II. INTRODUCTION

The brachiopod family Lingulidae contains two Cenozoic to Recent genera. These are: *Lingula* Cuvier, 1798, with seven Recent species ranging from tropical East and West Africa to Japan, New Zealand, and Hawaii (Emig, 1982) and *Glottidia* Dall, 1870, with four or five living Ameri-can species, one in the western Atlantic ranging from Chesapeake Bay to Florida, Louisiana, and the Caribbean; two species in the Baja California area, with one extending north to Monterey Bay; and one or two from Ecuador.

Paine (1963) noted numerous reports of fossil *Glottidia* from the Pacific coast of North America, beginning in the Eocene, and suggested that the genus may have originated in that area. However, Pajaud (1977) recognized the genus in the Triassic and Jurassic of Italy, and in the Cretaceous of Italy and Crimea. *Glottidia* also occurs in the Pliocene of Belgium and France (Chuang, 1964b; Pajaud, 1977). The Atlantic Coastal Plain localities documented in the present paper are Early Pliocene in age (Campbell, 1993).

III. RESULTS

Description: Detailed descriptions of *Glottidia inexpectans* may be found in Olsson (1914), Chuang (1964a), and Cooper (1988). It is an elongate, smooth, thin, fragile, compressed, phosphatic shell, very typical of lingulid brachiopods. *Glottidia inexpectans* shows allometric growth, embryonic shells being circular (Chuang, 1964a), juvenile specimens

developing elongate shells (figs. 1-3), and adults being proportionally broader (fig. 4). The brachial valve of *G. inexpectans* contains a single internal lamina just below the beak; the pedicle valve has two. Maximum length of *G. inexpectans* is 47 mm in Virginia (Cooper, 1988), and 56 mm in southern Florida (Florida Museum of Natural History collections, University of Florida, subsequently designated UF).

Outcrop occurrence: Olsson (1914) described *G. inexpectans* from fragmented specimens and one lot of over 20 five millimeter shells recovered from a paired specimen of *Chesapecten jeffersonius* found at Kingsmill, Virginia (UF loc. ZVOO6). The senior author discovered a second scallop shell refugium at Carter's Grove (UF loc. ZV008) containing 155 paired specimens averaging 13 mm (Table 1). Contents of the scallop pair were washed through a 0.5 mm screen to remove the fine sand matrix and all shell residue was examined. Brachiopod shells and shell fragments formed greater than 95 percent of the residue. In contrast, screened bulk samples of surrounding outcrop matrix yield mollusc shell residues with less than one percent brachiopod fragments. The *Glottidia* shells from Kingsmill and Carter's Grove were a light tan color, with an internal wash of white under the laminae. These Zone 1, Yorktown Formation (Sunken Meadow Member of Ward and Blackwelder, 1980) shells lack anoxic indicators such as micro-pyrite crystals, uniform shell blackening, or chemical degradation. Anoxic environments blacken phosphatic shell over a span of days to weeks (Kowalewski, 1996a). Zone 2 *Glottidia* in silt-clay sediment from Rice's Pit (UF loc. ZV004) and Yadkin (UF loc. ZV007) show tan banding alternating with blackened shell. Florida specimens (UF localities listed below) are similarly blackened with tan banding.

Associated Fauna: Campbell (1993) documented 233 species of lower Zone 2 molluscs from Rice's Pit. The senior author (in preparation) has documented some 220 molluscan species from the Zone 1, *Chama*-protected beds at Kingsmill and Carter's Grove.

Fauna contained with the juvenile *Glottidia* population inside the *Chesapecten* pair include a sparse assemblage of heart urchin spines from *Echinocardium orthonotum* (Conrad, 1843 [1844]), and unpaired valves of the bivalves *Cyclocardia granulata* (Say, 1824), *Modiolus pulchellus* Olsson, 1914, and *Astarte vaginulata* Dall, 1903. Olsson (1914) reported urchin spines, *M. pulchellus*, and a valve of *Diplodonta* in association with his encased *Glottidia.*

In Florida, most carbonate shell is leached from the Bone Valley deposits (UF loc. PO002 and UF loc. PO018), leaving

SIZE FREQUENCY OF SCALLOP-ENCASED *Glottidia inexpectans*

length (mm)	number of individuals
9	0
10	1
11	13
12	19
13	37
14	24
15	6
16	0

Brachial valves (one internal lamina) 155 specimens
Pedicle valves (two internal laminae) 156 specimens

Table 1: Frequency Table of maximum length for the population recovered from the scallop shell, and the proportion of brachial and pedicle valves.
Length is given for complete valves only.

the phosphatic brachiopods and a considerable vertebrate faunule. Some localities preserve interfingering Bone Valley phosphate sand and Tamiami limestone in outcrop (Morgan, 1994). Because our specimens are from spoil, we can not rule out the possibility of a Tamiami source, but the surrounding matrix has been typical of the Bone Valley member sand, and we believe that all *Glottidia* recovered from these localities are from the Bone Valley. At the Casa de Meadows pit (UF loc. CH026), calcitic shell is preserved. Occurring with *Glottidia* are molluscs including *Dicathais handgenae* Portell and Vokes, 1992, *Ecphora quadricostata* (Say, 1824), *Pterorytis umbrifer* (Conrad, 1832), *Urosalpinx (Vokesinotus) lepidotus* (Dall, 1890), *Euvola raveneli* (Dall, 1898), *Euvola hemicyclicus* (Ravenel, 1834), *Aequipecten muscosus* (Wood, 1828), *Argopecten* sp., *Amusium mortoni* (Ravenel, 1844), *Leptopecten leonensis* (Mansfield, 1932), *Nodipecten collierensis* (Mansfield, 1932), *Limaria caloosana* (Dall, 1898), *Ostrea sculpturata* Conrad, 1840, *Ostrea compressirostra* Say, 1824; the decapods *Calappa* sp. and a majid crab; barnacles including *Arossia glyptopoma* (Pilsbry, 1916), *Chesaconcavus tamiamiensis* (Ross, 1965), and *Tamiosoma advena* Zullo, 1992; and echinoids including *Arbacia improcera* (Conrad, 1843 [1844]) (= *A. crenulata* Kier, 1963), *Eucidaris tribuloides* (Lamarck, 1816), *Encope tamiamiensis* Mansfield, 1932, and *Echinocardium orthonotum* (Conrad, 1843 [1844]) (= *E. gothicum* (Ravenel, 1848)), (fauna from Portell and Vokes, 1992; Portell and Oyen, 1997; UF collections).

A second species of inarticulate brachiopod, *Discradisca lugubris* (Conrad, 1834) commonly occurs with *G. inexpectans* at Casa de Meadows, and at all Virginia localities. *Discradisca lugubris* is referred to *Discinisca* in most literature, but Cooper (1988) assigns it to *Discradisca*. *Discradisca lugubris* arose in the late Miocene in Virginia and survived into the Plio-Pleistocene Caloosahatchee Formation (UF collections).

Zoogeographic and Stratigraphic Distribution of Glottidia inexpectans: The Yorktown Formation (Pliocene) of the Virginia and northern North Carolina Coastal Plain was divided into a lower Zone 1 and an upper Zone 2 by Mansfield (1944). Ward and Blackwelder (1980) have further divided the Yorktown into four members. A general review of the stratigraphy and its complexities can be found in Campbell (1993). Scott (1988), Morgan (1994) and Allmon *et al.* (1996) provide detail for the Florida formations from which we here report *Glottidia*.

Hertlein and Grant (1944), Chuang (1964a), Cooper (1988), and Portell and Oyen (1997) are the only published records of this species subsequent to Olsson's original 1914 report. The type lot (Paleontological Research Institution 3518, 3519, 3520, and 3521) was collected from Zone 1 beds of the Yorktown Formation (Lower Pliocene), at Kingsmill, north bank of the James River near Williamsburg, Virginia. Subsequent collecting at the type locality confirmed an abundance of fragmented *Glottidia*. This exceptional outcrop has been destroyed by development in 1996. Previously unreported Zone 1 *Glottidia* localities include the spillway of Tutter's Neck Pond just east of Williamsburg, Virginia, and the bluffs at Carter's Grove approximately 1.5 km east of Kingsmill. The scallop-encased *Glottidia* population here reported (Plate 1, UF 81774) is from Zone 1 sands at Carter's Grove.

Chuang (1964a) redescribed the species based on an adult specimen from the lower Zone 2 beds of the Yorktown Formation at the Hampton Heights Dairy Pit. Subsequently, *Glottidia* have been recovered from laterally equivalent beds at Rice's Pit, Hampton, Virginia (Cooper, 1988, USNM 551520a-i; Virginia Museum of Natural History, and USC-Spartanburg collections) and at the Chesapeake Development Co. Pit (Yadkin, City of Chesapeake: USC-Spartanburg collections).

Portell and Oyen (1997) provided the first documentation of *G. inexpectans* outside Virginia. It is also present in the Raysor Marl near Cross, South Carolina (USC-Spartanburg collections; see LOCALITY DATA below).

IV. INTERPRETATION

Ecology of Recent Glottidia: Five species of Recent *Glottidia* have been documented (Dall, 1920; Emig, 1983). *Glottidia albida* (Hinds, 1844) was originally described from Magdalena Bay, Baja California, in 14 meters of water. This species may have a commensal slipper snail (*Crepidula nivea glottidiarom* Dall, 1905) on one or both valves (Dall, 1905; 1920). Keen (1971) synonymized *Crepidula nivea* C. B. Adams, 1852, with *Crepidula striolata* Menke, 1851, but made no mention of Dall's variety or of commensalism. The presence of commensal taxa suggests that *G. albida* is a shallow burrowing species. *Glottidia albida* has been recorded as far north as Monterey Bay, California. Recorded bathymetry ranges from intertidal to 477 meters (Jones and Barnard, 1963; Plaziat *et al.*, 1978).

Glottidia palmeri Dall, 1871, was described from the head of the Gulf of California, with additional records from southern California (Dall, 1920). It is common in lower intertidal mud flats in northeastern Baja California (Kowalewski, 1996a; Kowalewski and Flessa, 1994). Plaziat *et al.* (1978) record a bathymetry of intertidal to one meter. Dead shells of *in situ G. palmeri* are found at a depth of 10 to 20 cm below the sediment surface (Kowalewski (1996a:253).

Glottidia semen (Broderip, 1835) is a little-known Ecuadorian species based on an unique record dredged in 31 meters (Emig, 1983; Plaziat *et al.*, 1978). It may prove synonymous with one of the better-known species.

Glottidia audebarti (Broderip, 1835) was collected in hard, compacted, intertidal sand at a depth of 18 cm. Its type locality is Bay of Guayaquil, western Ecuador. Davidson (1888, posthumous) united *G. audebarti* with the western Atlantic *G. pyramidata* (Stimpson, 1860), a usage continued by Olsson (1914) and Crowder (1931). Dall (1920) showed the two taxa to be distinct. He speculated that after Davidson's death, an incorrect synonomy may have been rendered by the editors. Chuang (1964a) noted that Olsson compared his new fossil species with *G. audebarti* and *G. pyramidata*. Olsson (1914) compared his species with *G. audebarti* only in the sense that the western Atlantic *G. pyramidata* was considered a synonym. Plaziat *et al.* (1978) record a bathymetry for *G. audebarti* of intertidal to 13 meters.

Glottidia pyramidata (Stimpson, 1860) was described from muddy sand at low tide, Beaufort, North Carolina. Stimpson (1860) reported that Agassiz had a brachiopod specimen from the South Carolina coast. As *G. pyramidata* is the only coastal brachiopod in the area, we may assume that the Agassiz specimen is the first record from that state. Crowder (1931) gave a typical length of 27 mm and width of 10 mm, and reports specimens as "tidal, in vertical burrows, Cape Hatteras to Florida." Fox and Ruppert (1985: 44, 243, 270) reported *G. pyramidata* in mud burrows from protected beach at Debidue Island, South Carolina. They systematically sampled a set of habitats along the northern, central, and southern beaches of South Carolina, so the absence of *G. pyramidata* in two of the three areas sampled indicates patchy, disjunct distribution. Dall (1920) stated that Henderson found the species among the roots of sea grasses 2 feet below the water-sediment interface which would place them well below normal sampling efforts. However, Thayer and Steele-Petrovic (1974) used detailed observation and X-radiography to determine that the normal burrow is "U" shaped and no more than 5 cm deep. Paine (1963) suggests that the Henderson record may represent specimens buried by storm deposition. Alternatively, the Henderson report might be a lapse for "two feet of water." Recorded range is from Hampton and Fort Wool, Virginia, to southern and western Florida, Puerto Rico, and Louisiana (Cooper, 1973; Emig, 1983; Paine, 1970). Life span is about 20 months (Rudwick, 1970). In Florida, colonies of *G. pyramidata* are subject to predation by Tonguefish (*Symphurus plagiusa*) (Cooper, 1973), by Gulf Sturgeon (*Acipenser oxyrinchus desotoi*) (Mason and Clugston, 1993; UF collections), and by larger shorebirds such as Willets (*Catoptrophorus semipalmatus*) (Paine, 1962, 1963). Although sturgeon feed indiscriminately on shallow infaunal organisms (Gilbert, 1989), one sturgeon contained over 500 *G. pyramidata* (UF collections).

Paine (1962) reported up to 90 per cent infection of *G. pyramidata* by a gymnophalline metacercaria trematode larvae, but dismissed the Willet as host of the adult trematode due to a lack of infesting organisms. The records here cited suggest that fish may possibly be host to the adult parasite. Plaziat *et al.* (1978) recorded a bathymetry for *G. pyramidata* of intertidal to 73 meters.

Paine (1963) provided a thorough analysis of the ecology of *G. pyramidata*. Spawning is coincident with spring tides which maximizes offshore transport of larvae. *Glottidia* larvae were a common component of the plankton, and after three weeks of development were swept by the tides and currents into the shallow sublittoral and littoral areas where they settled in optimal habitats, most frequently in sand stabilized by sea grass. Paine (1963) also records planktic "drift larvae" well removed from "optimal habitat" and presumably lost. More recent works document offshore populations in 40 m (Paine, 1970) and 73 m (Cooper, 1973), suggesting that *G. pyramidata* is sparingly distributed across the shelf, but as an infaunal species is rarely collected in deeper waters.

Based on these records, *Glottidia* appears to be most common in intertidal to shallow subtidal tropical and subtropical protected muddy sands where it creates straight (Kowalewski, 1996a) or "U"-shaped burrows. When feeding, the animal creates a diagnostic pattern of one large oval hole flanked by two smaller holes (Rudwick, 1970).

Paleontology and Paleoecology of Glottidia inexpectans: We report a range for *G. inexpectans* essentially congruent with that of the Recent *G. pyramidata*. In both species, southern Florida specimens are larger than more northern populations. *Glottidia pyramidata* grows continuously until death at about 20 months (Paine, 1963). Growth and spawning are interrupted by winter temperatures in the Carolinas and northern Florida populations, but are continuous throughout the year in the southern Florida populations (Paine, 1963). Consequently, southern populations produce larger animals (Dall, 1920). Allmon *et al.* (1996) document upwelling as a nutrient source for the rich Lower and Middle Pliocene faunas of southern Florida. This increase in nutrients should improve diet for the filter-feeding *Glottidia*, further promoting maximum growth. Consequently, size differences between the Virginia and Florida populations are ecologic rather than taxonomic, and all Pliocene lingulid populations from Virginia to Florida are interpreted as representing *G. inexpectans*.

Although the Eocene to Recent distribution of *Glottidia* in the eastern Pacific is semicontinuous (Hertlein and Grant, 1944; Paine, 1963), the distribution of fossil *Glottidia* in the Atlantic and Gulf Coastal plains is disjunct, consisting of *G. glauca* Chuang, 1964c, rare in the lower Claibornian Eocene of Texas (Chuang, 1964c); *G. inexpectans* in the Lower Pliocene, Virginia to Florida; and *G. pyramidata* in the Recent. The lack of continuum may be real, or may be an artifact of selective taphonomic destruction (Kowalewski, 1996b). Lingulids are not likely to be preserved unless catastrophically buried (Kowalewski, 1996a, 1996b). The distribution of Recent *Glottidia* (Plaziat *et al.*, 1978), and their reproductive biology (Paine, 1963) argue for shallow water, coastal habitat, an environment rarely preserved in the Oligocene, and only occasionally in the Miocene of the Atlantic Coastal Plain. However, much of the Pleistocene deposition preserved in the Carolinas and Florida is beach and intertidal to shallow subtidal habitat seemingly well suited for *Glottidia*. Alternatively, during the Pleistocene, numerous tropical and subtropical invertebrate genera retreated to Caribbean refugia. *Glottidia* are conspicuously missing in the Caribbean Cenozoic (Cooper, 1955; Harper *et al.*, 1995, 1997; Emily Vokes, 1996, pers. comm.). This lack of evidence for Caribbean refugia and lack of intervening populations, even when prime lingulid habitat and exceptional preservation occur, suggest that the species of Western Atlantic *Glottidia* may represent independant colonizing events. However, the extinction of *G. inexpectans* approximately coincides with the closing of the Isthmus of Panama, and a western Atlantic refugium

seems more parsimonious than Holocene recruiting of eastern Pacific stock across the land-bridge.

Mortality: The scallop-enclosed population recovered in this study averaged 13 mm (Table 1). The assemblage forms a tight cluster with normal distribution around the mean. Olsson (1914) reported a similar scallop-enclosed population averaging about 5 mm. The uniform size in the two juvenile populations strongly suggest mass mortality. In our specimens, the brachiopods were recovered from within closed valves of *Chesapecten jeffersonius*, which were partially filled with fine sand. The plane of commissure was parallel to bedding, and the scallop appeared to be in life position. This suggests that the scallop shell was slightly gaping in quiet water and partially filled with sediment. The *Glottidia* larvae settled in a single spatfall, colonized the shell, and then died of starvation or oxygen deprivation after the scallop valves closed, either by relaxation of the ligament, or by burial of the shell. Starvation seems more likely because the shells lack anoxic indicators such as micro-pyrite crystals, shell blackening, or chemical degradation. Alternatively, articulated pairs may have washed into the shell. However, juvenile *Glottidia* shells are selectively destroyed upon reworking, and brachial valves are more subject to fragmentation than pedicle valves during transport (Kowalewski, 1996a). Also the sediment surrounding the scallop shell yielded a different faunule with abundant small disarticulated clam shells, but few brachiopods.

Paine (1963) determined that the vast majority of *Glottidia* die as larvae. Survivors preferentially populate sea grass beds, achieving a maximum density of greater than 1300 per square meter (Kowalewski, 1996a). The scallop-enclosed population of *G. inexpectans* here reported contained 156 individuals in a 15 cm diameter, circular shell. The area of containment is therefore 0.057 square meters which projects an equivalent population density of 2737 animals per square meter. This density is too great to be explainable by random drift of passive larvae. Settling *Glottidia* larvae are photonegative (Charles Thayer, 1996, pers. comm.), and those settling near a large, gaping bivalve with horizontal commissure would find the shadow attractive. Lingulids attach their pedicles to the base or wall of their

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PLATE 1

Figures

1-5. *Glottidia inexpectans* Olsson, 1914.
1. UF 81774, length 13.9 mm, pedicle valve from *Chesapecten*-enclosed population. UF loc. ZV008.
1a. External surface (note more pointed apex).
1b. Internal view showing double laminae.
2. UF 81774, length 14.4 mm, another pedicle valve from enclosed population. UF loc. ZV008.
2a. External surface.
2b. Internal detail.
3. UF 81774, length 13.7 mm, brachial valve from enclosed population. UF loc. ZV008.
3a. External surface (note rounder apex of valve).
3b. Internal view showing single lamina.
4. UF 11840, fragment length > 35 mm. Note predatory gastropod bore hole. UF loc. PO002.
5. UF 11840, nearly complete pedicle valve. Length 56 mm. UF loc. PO002.
6. *Chesapecten jeffersonius* (Say, 1824). Pair containing the *Glottidia* population. Maximum width 156 mm, maximum height 142 mm, average diameter 149 mm. UF loc. ZV008.
6a. Right valve UF 81775.
6b. Left valve UF 81775.

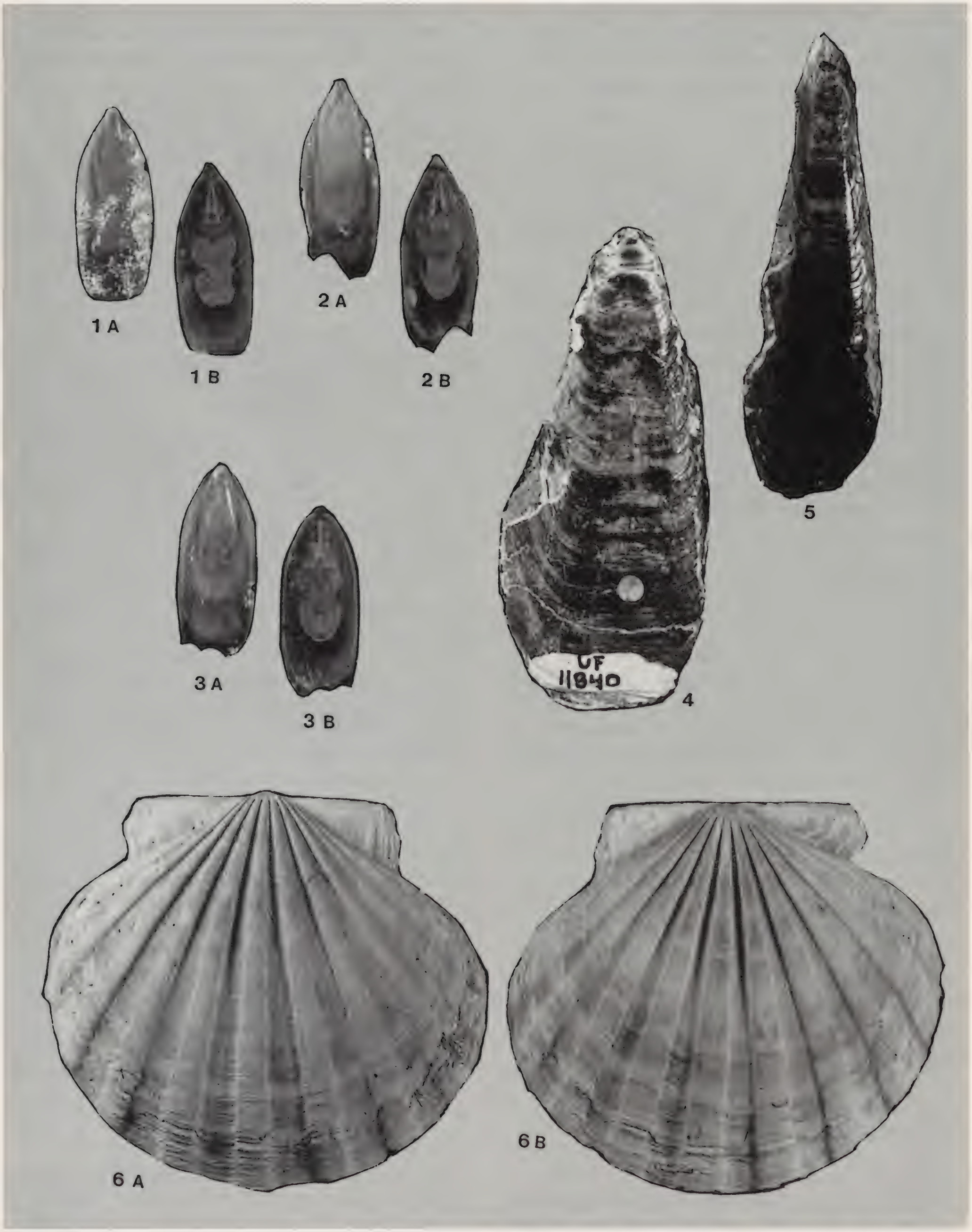

PLATE 1

mud-sediment burrows, not to a solid substrate like articulate brachiopods (Rudwick, 1970). In *Glottidia*, pedicle attachment to buried shell is fortuitous (Paine, 1963). Consequently, shadow rather than hard attachment substrate appears to be the attractant responsible for scallop shell colonization. The absence of specimens smaller than 10 mm in length may indicate high post-settling survival rates up to the mortality event. Alternatively, the smaller juvenile shells may have chemically disintegrated within their burrows while the scallop valves were open and normal circulation and sea-water chemistry were operative (Kowalewski, 1996a). We conclude that the shell-interior habitat proved initially optimal, but ultimately detrimental. Mass mortality of the juvenile population was most likely coincident with the closure of the host shell. Shell content of a second large, closed *Chesapecten* was compared with that of its immediately adjacent sediment. In both, fine sand made up 95 percent of the sediment. Scant mollusc shell fragments dominated the screened residue. The shell-encased sediment included a single beak fragment of *Glottidia*. Apparently, *Glottidia* invasion of a scallop shell was uncommon, opportunistic and probably seasonal. Additional studies are needed to determine the frequency of brachiopod colonization.

Gastropod predation of Recent *Glottidia* was first documented by Kowalewski and Flessa (1994). Rare Florida specimens of *G. inexpectans* show evidence of similar attacks (Plate 1, fig. 4).

Paleobathymetry: The paleobathymetry of the Zone 1 deposits at Kingsmill and Carter's Grove is equivocal. An ongoing study of the molluscan taxa has yielded over 220 species, with genera most typical of water depths of 40 to 60 meters, based on recent data from Porter (1974). The topography and distribution of Zone 1 sediments are are also compatible with a bathymetry of 40 to 60 meters. The substantial otolith fauna from Kingsmill deposits suggests depths of over 100 meters (Robert Lavenberg, 1995, pers. comm.). By the measure of Recent intertidal *Glottidia* species, *G. inexpectans* appears to have an anomalous depth distribution. It is equally possible that the Recent *Glottidia* have been sampled only in the shallowest part of their normal range. Species which live in deep burrows beyond the littoral zone remain poorly sampled. The reports of Jones and Barnard (1963), Paine (1970), Cooper (1973), and Plaziat *et al.* (1978) confirm open shelf occurrences for Recent *Glottidia*. Shallow, subtidal environments are known in the lower Zone 2 Yorktown beds at Petersburg, Virginia, but no *Glottidia* have been recovered from that area.

In contrast, the southern Florida assemblage at the Casa de Meadows pit yields two good bathymetric indicators. Recent *Dicathais* prefer rocky or hard ground substrates in very shallow subtidal waters, and *Aequipecten muscosus* is most frequently found in 10 to 40 meters. We suggest deposition in subtidal to 20 meters. Consequently, the Casa de Meadows specimens may represent the shallow water populations missing from the Virginia Pliocene. The Bone Valley sites (UF loc. PO002, UF loc. PO018) are devoid of other invertebrate species, but their vertebrates include terrestrial taxa (UF collections), which are more consistent with shallow, near-shore deposition (Morgan, 1994).

Taphonomy: The taphonomy of *Glottidia palmeri* was thoroughly studied by Kowalewski (1996a). He documents rapid disintegration of brachiopod shells in *in situ* burrows, found in intertidal, and supratidal environments. His study provides insights, but little data for the most commonly preserved marine habitat, the subtidal shelf environment. Kowalewski (1996, pers. comm.) states that efforts were made but the turbidity of the Gulf waters made study impossible. Consequently, *G. inexpectans* may fill this key gap in our knowledge of lingulid taphonomic pathways.

Glottidia valves are exceedingly thin and fragile. Dall (1920) observes that tissue shrinkage upon death and air-drying was sufficient to fracture the valves of *G. pyramidata*. Dead shells are often destroyed within their burrows by chemi-

cal degradation associated with decay (Paine, 1963; Kowalewski, 1996a). Although the shells of the Pliocene species thickened with growth, the largest specimens remained thin and fragile. Subtidal decay and transport were normally sufficient to fragment shells of all growth stages. *Glottidia inexpectans* are most common in screened and floated residue of Zone 1 fine sands. The shells are invariably broken perpendicular to the long axis, and only beak fragments or the distal quarter of the shells are typically recovered. Although care was exercised in the excavation and screening of the Zone 1 sediment, further fragmentation during the sample processing cannot be ruled out. We believe that we are observing predepositional fragmentaton because careful search of outcrop has yielded no complete-but-broken specimens, and because the more fragile middle sections of the shell are rare or absent from the screened residue. Paired adult individuals have been found imbedded in silt-clay deposits of the lower Zone 2 beds in Virginia. *Glottidia* have been observed in Zone 2 sands only at Claremont Wharf, south bank of the James River (Warren Blow, 1996, pers. comm.). Kowalewski (1996a) found that deep burial, either by rapid sedimentation or catastrophic means was necessary to place the *Glottidia*-bearing deposit below the Taphonomic Active Zone. The Yorktown Formation in Virginia contains numerous examples of tempestite storm deposition and some "Lagerstatten" deposits in which bivalves are paired, crabs have articulated limbs, echinoids have associated spines, and shell preservation down to minute and fragile pteropod molluscs is perfect. No *Glottidia* have been recovered from these deposits. Its presence in silt-clay might reflect habitat preference, but that hypothesis is negated by its greater abundance in the fine sands of Zone 1. We conclude that subtidal taphonomic destruction of *Glottidia* shells was as rapid and effective as that documented for the intertidal and supratidal zones.

Despite rapid burial and the structural protection from the paired valves of a large, heavy *Chesapecten* shell, only 32% (100 of 311) of the exceptionally preserved *Glottidia* valves were unbroken. Dorsal valves were more frequently broken than ventral, suggesting variable strength. Valves retained within the scallop show no chemical degradation. The pervasive valve destruction in the unsheltered sand environment accentuates the contrast with the exceptionally preserved, scallop-enclosed population. Once entombed, the *Chesapecten* shell protected the *Glottidia* valves from further taphonomic destruction.

Post-depositional taphonomy appears to be important in the preservation of *Glottidia.* In Virginia and northern North Carolina Zone 1 sediments are typically well sorted, fine sand which is highly permeable, forming a shallow aquifer. Shell carbonate is a small fraction of the bulk sediment. The flow of fresh groundwater has partially to completely leached aragonitic shell from the sediments, leaving calcitic shell, and occasional phosphatic remains, mostly bone. Along the north shore of the James River from Kingsmill to Carter's Grove, the Zone 1 beds are capped by a massive Zone 2 *Chama* reef which is greater than 80 per cent carbonate and as much as 10 meters thick. Groundwater percolating through this cap becomes less acidic, and the protected underlying Zone 1 faunas have exquisite preservation of even the most minute aragonitic species. Consequently, post-depositional chemical degradation removed both aragonitic shell and phosphatic *Glottidia* from the leached sediments. In Virginia, the destruction of *Glottidia* was complete in all stages of growth; in Florida, the juvenile specimens were selectively removed.

V. SUMMARY AND CONCLUSIONS

Glottidia inexpectans Olsson, 1914, is found in Early Pliocene beds from Virginia to Florida. The species attained a larger maximum size in Florida, paralleling the pattern in the Recent *G. pyramidata*. The proclivity of *G. inexpectans* for shell degradation paralleled that of the more thoroughly studied Recent species such as *G. pyramidata* and *G. palmeri*, which typically disintegrate within a few weeks of death. Preservation of specimens in any

numbers must combine structural integrity with protection from chemical deterioration. The 155 pairs of juvenile *G. inexpectans* here reported and the smaller population reported by Olsson (1914) were preserved within paired valves of *Chesapecten jeffersonius,* a large species of scallop with thick, well-inflated valves. The added protection afforded by this microhabitat appears essential for preservation of unbroken, subadult shells in sand. Stiff silt-clay beds of lower Zone 2 Yorktown and leached silty sand deposits of southern Florida occasionally preserve broken adult *Glottidia* imbedded in matrix.

Glottidia inexpectans has been recovered from mid-shelf assemblages in Virginia indicative of a paleobathymetry of 40 to 60 meters. The Florida assemblage seems indicative of shallower waters, perhaps subtidal to 20 meters.

Glottidia species have been documented from the Atlantic Coastal Plain and Gulf Coast Eocene, Pliocene, and Recent. The stratigraphic gap between the Eocene and Pliocene *Glottidia* may be real, rather than an artifact of taphonomic megabias (Kowalewski, 1996b). However, the western Atlantic and eastern Pacific populations have been physically separated since the Middle Pliocene, necessitating an Atlantic origin for the Recent species.

The exceptional occurrence of abundant paired juvenile *Glottidia* indicates an unusual taphonomic event. *Glottidia* larvae settled in a single spat-fall, colonized a gaping scallop shell, and then died of starvation after the valves closed. Reworking is unlikely because juvenile shells are fragile, pedicle valves are more subject to breakage, and the fauna of the contained sediment differs substantially from that surrounding the scallop shell.

V. ACKNOWLEDGMENTS

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VI. LOCALITY DATA

The following are collecting localities of the Invertebrate Paleontology Division, Florida Museum of Natural History, University of Florida (UF).

VIRGINIA

ZV004 Rice's Pit. Shell pit off Fox Hill Road, Hampton, Virginia. (Hampton Quadrangle, USGS 7.5 minute series, 37 degrees, 03 minutes, 37 seconds north, 76 degrees, 14 minutes, 33 seconds west). Lower Zone 2, Yorktown Fm.

ZV006 Kingsmill 01. North bank of James River, 100 meters east of the Marina at Kingsmill Estates, just southeast of Williamsburg, Virginia. (Hog Island Quadrangle, USGS 7.5 minute series, 37 degrees, 13 minutes, 05 seconds north, 76 degrees, 38 minutes, 45 seconds west). Zone 1, Yorktown Fm.

ZV007 Chesapeake Development pit. End of Cooke's Mill Road, between the communities of Yadkin and Deep Creek, Chesapeake, Virginia. (Norfolk South Quadrangle, USGS 7.5 minute series, 36 degrees, 45 minutes, 13 seconds north, 76 degrees, 22 minutes, 05 seconds west). Lower Zone 2, Yorktown Fm.

ZV008 Carters Grove 01. North bank of James River, Carter's Grove Plantation, 4 km southeast of Williamsburg, Virginia. (Hog Island Quadrangle, USGS 7.5 minute series, 37 degrees, 12 minutes, 35 seconds north, 76 degrees, 38 minutes, 02 seconds west). Zone 1, Yorktown Fm.

ZV009 Tutters Neck Dam 01. Spillway of Tutter's Neck Dam, Williamsburg, Virginia. (Williamsburg Quadrangle, USGS 7.5 minute series, 37 degrees, 15 minutes, 05 seconds north, 76 degrees, 41 minutes, 10 seconds west). Zone 1, Yorktown Formation.

SOUTH CAROLINA

ZS013 Lockheed Martin Berkeley County Quarry. Six km south of Rt. 6, on Rt. 59 between Eutaw Springs and Cross, South Carolina. (Cross Quadrangle, USGS 7.5 minute series, 35 degrees, 21 minutes, 08 seconds north, 80 degrees, 14 minutes, 04 seconds west). Raysor Marl.

FLORIDA

CH026 Casa de Meadows 02. Shell pit approximately 1.2 km east of Grove City, Charlotte County, Florida (NE 1/4, NE 1/4, Sec. 16, T41S, R20E; Englewood Quadrangle, USGS 7.5 minute series). Lower Tamiami Fm.

PO002 Ft. Green #13 Dragline. Sand and phosphate pit approximately 6 km south of Bradley Junction, Polk County, Florida (NE1/4, Sec. 2, T32S, R23E; Baird Quadrangle, USGS 7.5 minute series). Bone Valley Member, Peace River Fm.

PO018 Palmetto Mine. Sand and phosphate pit approximately 5 km northeast of Baird, Polk County, Florida (E 1/2, Sec. 9, T32S, R24E; Baird Quadrangle, USGS 7.5 minute series). Bone Valley Member, Peace River Fm.

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A NEW GENUS, *MARTINETTA*, AND TWO NEW SPECIES OF XANTHOID CRABS FROM THE MIDDLE EOCENE SANTEE LIMESTONE OF SOUTH CAROLINA

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I. ABSTRACT

Two new xanthoid crabs, *Martinetta palmeri,* new genus and new species, and *Eohalimede saundersi,* new species, are described from the middle Eocene Santee Limestone of South Carolina. *Martinetta palmeri* is thus far the largest middle Eocene crab known to occur in the Carolinas. *Eohalimede saundersi* is the second species of this genus described. *Sarahcarcinus campbellorum* is transferred from the family Cancridae to the family Portunidae.

II. INTRODUCTION

In the summer of 1995, Lauck W. Ward brought several pieces of a single large xanthoid crab to the attention of the first author. His specimen had been collected some years earlier from the Santee Limestone at the Martin Marietta Georgetown Quarry, Georgetown Co., South Carolina. It represented a crab considerably larger than any that we had yet seen from the Santee Limestone, but it was so fragmentary that it could not be identified to genus. We suspected it might belong to the Old World fossil genus *Harpactocarcinus* A. Milne-Edwards, 1862. In October 1996, Mr. Billy T. Palmer, Sr., of Goose Creek, South Carolina, brought a second large, very well-preserved specimen of this same taxon to our attention. Mr. Palmer had collected this specimen from the Martin Marietta Berkeley Quarry, Berkeley Co., South Carolina. Though strikingly similar in outline and anterolateral dentition to *Harpactocarcinus,* this specimen obviously represented a new genus and species, *Martinetta palmeri,* which could be distinguished from the former on the basis of its much smaller front and V-shaped orbit alone. This new crab represents the largest crab species found in middle Eocene deposits of the Carolinas. In size it is challenged only by the much more common *Eocarpilius carolinensis* Blow and Manning, 1996, with which it co-occurs in the Santee Limestone, and *Menippe burnsi* Rathbun, 1935, from the Castle Hayne Limestone.

A second species of *Eohalimede* Blow and Manning, 1996, was also brought to our attention by Mr. Palmer in October. This new species, *E. saundersi,* is represented by two very well-preserved carapaces that are conspecific with our poorly preserved paratype of *E. walleri* Blow and Manning, 1996. The single paratype (USNM 484581) of *E. walleri* is therefore transferred to our new species, *E. saundersi.* The frontal and fronto-orbital proportions given for the type species of *Eohalimede, E. walleri,* are uncertain in that they were based solely on the paratype. The holotype, and now only known specimen of *E. walleri,* is truncated anteriorly just behind the front and orbits.

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The genus *Sarahcarcinus* Blow and Manning, 1996, is transferred from the family Cancridae to the family Portunidae. This reassignment is based on a single specimen also provided by Mr. Palmer, which exhibits a portunid-like front and orbits, characters unavailable for study in formulating our original description.

Repositories: Holotypes and some paratypes are deposited in the National Museum of Natural History, Smithsonian Institution, Washington, D.C., and The Charleston Museum, Charleston, South Carolina. Some paratypes, where indicated, are deposited in the Virginia Museum of Natural History, Martinsville, Virginia.

Abbreviations:
ChM No. PI, The Charleston Museum, Invertebrate Paleontology Catalogue Number.

M.M., quarries owned and operated by Martin Marietta Aggregates.

NMNH, National Museum of Natural History, Smithsonian Institution.

USGS, the U.S. Geological Survey (when used with a number indicates a locality).

USNM, abbreviation for catalogue numbers of the former U.S. National Museum, now the National Museum of Natural History.

VMNH, Virginia Museum of Natural History.

Measurements: Expressed in millimeters as follows: cl, carapace length, maximum longitudinal measurement; cw, carapace width, maximum transverse measurement; prl, propodus length, length of palm or combined length of palm and fixed finger; prh, propodus height; prt, propodus thickness; l, length, overall; w, width, overall.

III. ACKNOWLEDGMENTS

We especially thank Billy T. Palmer, Sr., of Goose Creek, South Carolina for sharing his knowledge and collection of Santee Limestone crabs with us. We thank Albert E. Saunders of The Charleston Museum, Charleston, South Carolina, for bringing Mr. Palmer's collection to our attention and for making it available through The Charleston Museum for our study. We also particularly thank Lauck W. Ward of the Virginia Museum of Natural History, Martinsville, Virginia, for making his collection of Santee Limestone crabs available to us. Mrs. Jan Hester, registrar, The Charleston Museum, helped process the loan. Discussions between the first author, Gerald R. Baum of Texaco, Bellaire, Texas, and Francis M. Hueber of the National Museum of Natural History, Smithsonian Institution, Washington, D.C., added significantly to the content of this paper.

IV. SYSTEMATIC PALEONTOLOGY

Family MENIPPIDAE Ortmann, 1893
MARTINETTA, new genus

Diagnosis: Carapace large (cw exceeding 130 mm), transversely oval, strongly convex longitudinally, moderately convex transversely; length about 3/4 carapace width, broadest at anterolateral angle, regions weakly defined.

Fronto-orbital margin slightly less than 1/3 carapace width.

Front quadrilobate, width less than 1/4 carapace width, deflexed at about 45° along midline.

Orbit relatively small, marginal, V-shaped in dorsal view, composed of 4 lobes separated by three closed fissures; inner lobe eavelike, raised well above median and outer orbital lobes.

Basal antennal article relatively narrow, length slightly less than twice width, terminating well below inner angle of suborbital lobe.

Anterolateral margins without lobes or fissures, usually armed with 14 to 16 distinct denticles.

Protogastric and mesogastric regions distinctly elevated, forming broad platform.

Chelipeds unequal in males, right chela larger, massive, height of propodus about four-fifths length, distinctly highest distally.

Type Species: Martinetta palmeri, new species, by present designation and monotypy.

Etymology: This genus is named for Martin Marietta Aggregates in recognition of their considerable contribution to paleontology through their generosity in granting access to their commercial excavations which have provided so

many professional, student and amateur paleontologists with a much needed and enjoyed window to the past. Gender feminine.

Remarks: In dorsal outline and anterolateral denticulation, *Martinetta* very closely resembles the genus *Harpactocarcinus* A. Milne-Edwards, 1862, type species by orginal designation (p. 46), *H. punctulatus* (Desmarest, 1822). It can, however, be separated immediately from *Harpactocarcinus* on the basis of its proportionally small, V-shaped (in dorsal outline) orbits alone. In contrast, the orbits of *Harpactocarcinus* are proportionally much larger and semi-circular in shape. *Martinetta* also has a narrower front, and broader, more elliptical carapace outline than *Harpactocarcinus*. *Martinetta* can further be distinguished from *Harpactocarcinus* by its: 1) more transversely flattened carapace; 2) relatively longer anterolateral margin; 3) low, thin orbital margins, unlike the raised, thickened orbital margins of *Harpactocarcinus*; 4) distinctly elevated protogastric and mesogastric regions; and 5) much shorter and much higher distally, more quadrate, massive right chela.

Martinetta also appears to be considerably larger than the average specimen of *Harpactocarcinus*. Both of our specimens are about 20% to 25% larger than the largest of more than 300 specimens of *H. punctulatus* (including the type of Desmarest) and *H. jacquoti* A. Milne-Edwards, 1865, measured by Via (1969, p. 241-256).

The small V-shaped orbits and lack of deep branchial grooves, characteristic of *Martinetta,* easily distinguish it from the genus H*arpactoxanthopsis* Via, 1959, which is represented in the South Carolina middle Eocene by *H. carolinensis* (Rathbun, 1935).

In outline and general form, the right or major chela of *Martinetta* is similar to that found in the genus *Eocarpilius* Blow and Manning, 1996. However, the right chela of *Martinetta* can be easily distinguished from *Eocarpilius* as follows: 1) *Martinetta* has a strong spine on the superior distal margin of the carpus, which is lacking on the carpus of *Eocarpilius*; 2) the superior margin of the propodus of *Martinetta* is much straighter than that of *Eocarpilius*; and 3) the proximal tooth of the right propodus of *Martinetta* is much lower and shorter than the same tooth of *Eocarpilius*. In *Martinetta* the proximal tooth of the propodus is about one-third its length in contrast to one-half the length of the propodus in *Eocarpilius*.

To a lesser extent *Martinetta* is also somewhat similar to the extant genus *Menippe,* which is represented in the Middle Eocene Castle Hayne Limestone of North Carolina by *M. burnsi* Rathbun, 1935. This fossil species is based on an incomplete, large, left propodus (holotype USNM 371580) and a series of other partial chelae which do not appear to have been associated. In outline, the left propodus of the holotype of *M. palmeri* is very similar to that of the holotype or left propodus of *M. burnsi*, but unlike the latter where the left propodus is thickest proximally, in *M. palmeri* the propodus is thickest medially. In addition, the superior margin of the left propodus of *M. palmeri* is relatively smooth with a few very weak ridges along its inner surface. By contrast, the ridges found on both the inner and outer surfaces of the left propodus of *M. burnsi* are reticulated, more prominent, and much more extensive. No carapace or fragment thereof of the distinctive carapace of *Menippe* has thus far been reported from the carolinian Eocene. Members of both genera have proportionally small orbits and raised protogastric and mesogastric regions which form a platform. However, the continuous unbroken, denticulated margin of *Martinetta* easily distinguishes it from the deeply cut, lobate margin distinctive of *Menippe.*

MARTINETTA PALMERI, new species
(Plate 1, figure 1; text-figure 1)

Description: Carapace large (cw exceeding 130 mm), transversely oval, strongly convex longitudinally, moderately convex transversely; length about 3/4 carapace width, broadest just posterior to midline at anterolateral angle, regions very weakly defined.

Fronto-orbital margin slightly less than 1/3 carapace width.

Front quadrilobate, relatively narrow, width less than 1/4 carapace width, deflexed at about 45° along midline.

Frontal lobes subcarinate along lateral mar-

gins, submedian pair distinctly larger than lateral lobes; submedian lobes subparallel to midline, rounded in dorsal outline, close set, flattened, produced well beyond lateral lobes but not below dorsoventral plane; lateral lobes obliquely set to midline, laterally directed, subacute in dorsal outline, widely separated from submedian lobes, much thicker anteriorly than submedian lobes, each set clearly below inner orbital eave-like lobe and separated from the latter by a distinct lateral indentation.

Orbit relatively small, marginal, V-shaped in dorsal view, composed of 4 lobes separated by 3 closed fissures; inner lobe largest, eavelike, raised well above median and outer orbital lobes; outer orbital lobe about twice width of small median lobe and slightly greater than 1/2 width suborbital lobe; outer orbital angle defined by strong denticle, latter set just above anterolateral margin. Suborbital margin strongly concave, finely granulated below, inner angle subacute, strongly produced, visible in dorsal view.

Antennae incomplete; basal antennal article relatively narrow, lateral margins straight, subparallel, length slightly less than twice width, terminating well below inner angle of suborbital lobe. Basal article not reaching or in contact with lateral frontal lobe.

Antennule incomplete; basal article subtriangular in outline, outer lateral margin with weak carinae anteriorly, inner lateral margin with strong carinae. Article in contact with lateral margin of basal article of antenna along its entire length.

Anterolateral margins without lobes or fissures, strongly arched, converging anteriorly, slightly upturned at anterolateral angle; margins rounded, moderately thick, armed with 14 to 16 distinct, subconical, upturned denticles of subequal size; denticles usually equidistant, sometimes paired; posteriormost pair widely separated from denticle at anterolateral angle; latter strongest of all marginal denticles, distinctly upturned. Dorsal and ventral margins, where unweathered, smooth with scattered punctae; denticles and surfaces near anterolateral angle finely granulate; ventral surfaces just below denticles finely granulate.

Posterolateral margins weakly sinuous in dorsal outline, strongly convergent posteriorly, length about 4/5 length of anterolateral margins. Margins sightly concave anteriorly where steep; slightly convex, inflated posteriorly.

Posterior margin very weakly convex in dorsal outline, width (estimated) less than 2/3 width of front; margin defined by very low, smooth, flattened, narrow, rim.

Dorsal surface without distinct grooves, regions ill defined, surfaces where unweathered, punctate; surfaces of front, orbits and anterolateral margin appear finely granulate.

Protogastric and mesogastric regions distinctly elevated forming broad platform, margins convergent posteriorly; platform weakly sulcate anteriorly along midline, bordered posterolaterally by shallow depressions.

Urogastric and cardiac regions weakly defined by shallow depression formed by epimeral muscle scars. Urogastric region weakly elevated, badly weathered; cardiac region with two widely spaced, laterally placed, small circular pits, surface otherwise smooth, flattened transversely, very weakly sulcate along midline.

Posterior gastric pits distinct, though small, circular, closely spaced, visible just anterior to epimeral muscle scars.

Intestinal region broader than long, moderately elevated, weakly separated from cardiac region, distinctly separated from branchial regions by broad, shallow grooves.

Pterygostomian region, where adjacent to buccal cavity, broader than subhepatic margin, surface smooth.

Buccal cavity subquadrate, width slightly less than 1/4 carapace width.

Third maxilliped broken, incomplete. Merus about 2/5 length of ischium, concave laterally, raised medially, with shallow, narrow depression along inner margin. Ischium ill-defined, fragmentary.

PLATE 1

1. *Martinetta palmeri* Blow and Manning, n. gen. and sp.
   1a. Male holotype, articulated specimen in dorsal view, (USNM 496363), cl 91.9 mm, cw 126.7 mm; right propodus prl 106.4 mm, prh 56.1 mm, prt 31.5 mm; left propodus prl 78.1 mm, prh 30.7 mm, prt 19.9 mm. Scale = 20 mm.
   1b. Male holotype above in ventral view. Scale = 20 mm.

Locality: M.M. Orangeburg Quarry, Orangeburg Co., South Carolina. Santee Limestone.

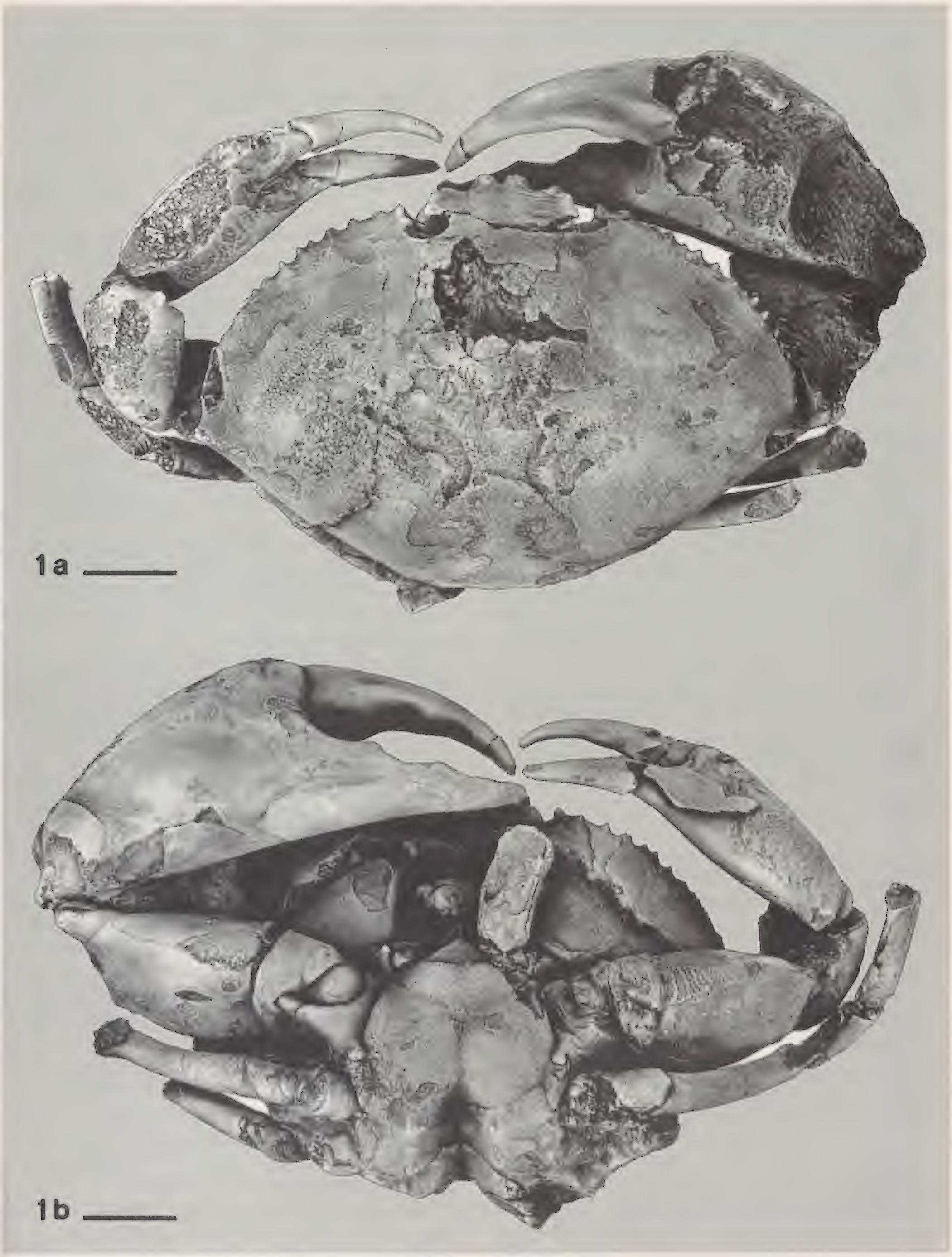


PLATE 1

Mandibles visible, broken distally, otherwise covered.

Sternum of male relatively narrow, about 1/3 carapace width, lateral margins convergent posteriorly, sternites 7, and particularly 8, very narrow.

Abdomen lacking, width (estimated) about 1/2 width of sternum, with somites broadening gradually posteriorly as inferred from outline of narrow, deep, abdominal depression.

Chelipeds unequal in males, right or major chela about twice the size of the left or minor chela. Surfaces of both right and left chelipeds punctate and very finely granulate. Most surfaces appear smooth to the unaided eye.

Meri of chelipeds short, length of each subequal to length of associated carpi, each distinctly highest distally; outer surface inflated, punctate with fine granules; inner surface concave, very smooth with few small punctae and very few fine granules. Superior margin strongly arched in lateral and dorsal views; margin narrow, rounded. Inferior margin broad, flattened. Punctae appear most concentrated on outer surface adjacent to inferior margin; granules appear most concentrated along superior margin and distally adjacent to insertion of carpus at superior and inferior angles.

Carpi of chelipeds strongly inflated, flattened near inferior distal margin; superior distal margin armed with a single, strong, obliquely directed spine; spine situated between superior point of articulation with propodus and strong, inner carpal angle; latter swollen, blunt, rounded.

Propodus of major or right cheliped of male massive, height of palm about 4/5 its length, highest distally, steeply sloping proximally; superior margin weakly arched; surface of entire palm densely granulate; outer surface with scattered punctae, most concentrated along or near superior and inferior surfaces; inner surface with weak reticulated ridges near superior margin. Fingers about 4/5 length of palm, subequal in length, widely gaping along entire length; fixed finger in dorsal view moderately deflected inward along entire length, nearly straight in lateral view along inferior margin; superior surface with 2 large, subequally spaced, molariform teeth; first or proximalmost tooth about 1/3 length of finger, largest, broad, greatly elevated distally, stepping down vertically to second, smaller tooth; second tooth about 3/4 width of first, blunt, very rounded marginally, steeply elevated above distal third of finger; tip of finger moderately upturned, obtuse; moveable finger in dorsal view deflected inward along distal third, in lateral view moderately arched along superior margin; inferior surface with 2 closely spaced, molariform teeth; first or proximalmost, largest, set in opposition to first tooth of fixed finger; second about 1/2 size of first, obtuse, set to fall between first and second teeth of fixed finger.

Propodus of minor or left cheliped of male much smaller than that of major, height of palm about 3/5 length, highest distally, superior surface gently sloping proximally; surfaces of palm badly eroded, fragment of original surface punctate and densely granulate. Fingers of subequal length, 3/5 length of palm; fixed finger deflected downward and inward; superior surface with at least three badly abraded teeth; first or proximalmost obtuse, second highest and like third, subcarinate; distal third of superior surface lacking; tip of finger, obtuse, weakly upturned; moveable finger moderately deflected downward and inward; inferior surface lacking proximally; surface with two subcarinate teeth, proximalmost highest; teeth set to fall in opposition on either side of second or largest tooth of fixed finger; tip of finger obtuse.

Ambulatory legs 1, 2 and 3? present, incomplete; length of 1st excluding dactylus slightly more than 2/3 width of carapace; length of merus of 1st leg about twice length of carpus and 1 1/2 times length of propodus; length of meri of each leg gradually decreasing posteriorly; meri compressed laterally, inner surfaces curved gently forward [anteriorly]; superior surface of legs finely granulate, other surfaces smooth with scattered punctae.

Description of the dorsal aspect of the carapace based principally on paratype ChM No. PI 15214. Description of the ventral aspect of the carapace and the chelipeds based principally on the male holotype. Both specimens are partially articulated with most of their respective cuticles intact.

Etymology: This species is named for the collector of the holotype Mr. Billy T. Palmer, Sr., United States Navy, Retired, who brought it to our attention and in recognition of his volunteer work and extensive collecting efforts for The Charleston Museum.

Holotype: Nearly complete male carapace with articulated chelipeds and ambulatory legs (USNM 496363) cl 91.9 mm, cw 126.7 mm (spines at anterolateral angle missing); estimate of cw complete, 131.0 mm; incomplete right propodus (superior margin missing along

Text-figure 1. *Martinetta palmeri* Blow and Manning n. gen. and sp. Paratype, right frontal lobes and orbit in dorsal view, (ChM No. PI 15355), estimated cw 140.0 mm. Scale = 4 mm.

Locality: M.M. quarry SE of Jamestown, Berkeley Co., South Carolina. Santee Limestone.

distal half) prl 106.4 mm, prh 56.1 mm, prt 31.5; incomplete left propodus (superior margin broken, nearly complete) prl 78.1 mm, prh 30.7 mm, prt 19.9 mm.

Type Locality: M.M. Orangeburg Quarry, Orangeburg County, South Carolina. Santee Limestone.

Paratypes: Incomplete carapace with fragments of sternum and articulated right merus and incomplete left cheliped (ChM No. PI 15214) cl 95.2 mm, cw 130.3 mm (left margin eroded, nearly complete) estimate of cw complete to tips of denticles 140.0 mm; right merus (nearly complete) l 45.6 mm; left propodus prl 34.3 mm, prh 14.5 mm, prt (covered). M.M. Berkeley Quarry, Berkeley County, South Carolina. Santee Limestone.

Associated weathered right and left halves of incomplete carapace (VMNH 904). Fragmentary right half of carapace including partial orbit, anterolateral margin with adjacent ventral surface and pterygostomian region intact, and articulated merus with fragments of carpus and propodus present, cw 86.7 mm, estimated cw of entire carapace, if complete, 165.0 mm; right merus l 38.8 mm; fragment of left half of carapace including partial anterolateral margin with adjacent ventral and pterygostomian region surfaces, overall length of fragment 48.2 mm; M.M. Georgetown Quarry, Georgetown Co., South Carolina. Santee Limestone.

Carpus and propodus of right or minor cheliped (ChM No. PI 15295) combined length of both [carpus and propodus] 108.3 mm, prh 38.7 mm, prt 24.9 mm. Incomplete carpus and propodus of right cheliped, fingers lacking (ChM No. PI 15296) prl (to base of fixed finger) 61.0 mm, prh 53.2 mm, prt 29.9 mm. Incomplete right or major propodus with associated incomplete front, right orbit, and about half? of the right anterolateral margin of carapace (ChM No. PI 15355) prl (incomplete, proximal end missing) 105.3 mm, prh (incomplete, superior margin missing) 56.5 mm, prt (incomplete, cuticle of inner surface missing) 35.1 mm. (ChM Nos. PI 15295, PI 15296 and PI 15355) M.M. Quarry SE of Jamestown, Berkeley Co., South Carolina. Santee Limestone.

Occurrence: Santee Limestone, South Carolina.

Remarks: Of the two large crabs known to co-occur in the Santee Limestone, *Martinetta palmeri* and *Eocarpilius carolinensis,* carapaces of the latter are by far the more common. The three articulated specimens of *M. palmeri* on which our description is based and two or three others collected or seen by Mr. Palmer are the only specimens of this large crab known to the authors.

Family XANTHIDAE MacLeay, 1838

XANTHIDAE MacLeay, 1838, p. 59 [name on *Official List*].

EOHALIMEDE Blow and Manning, 1996

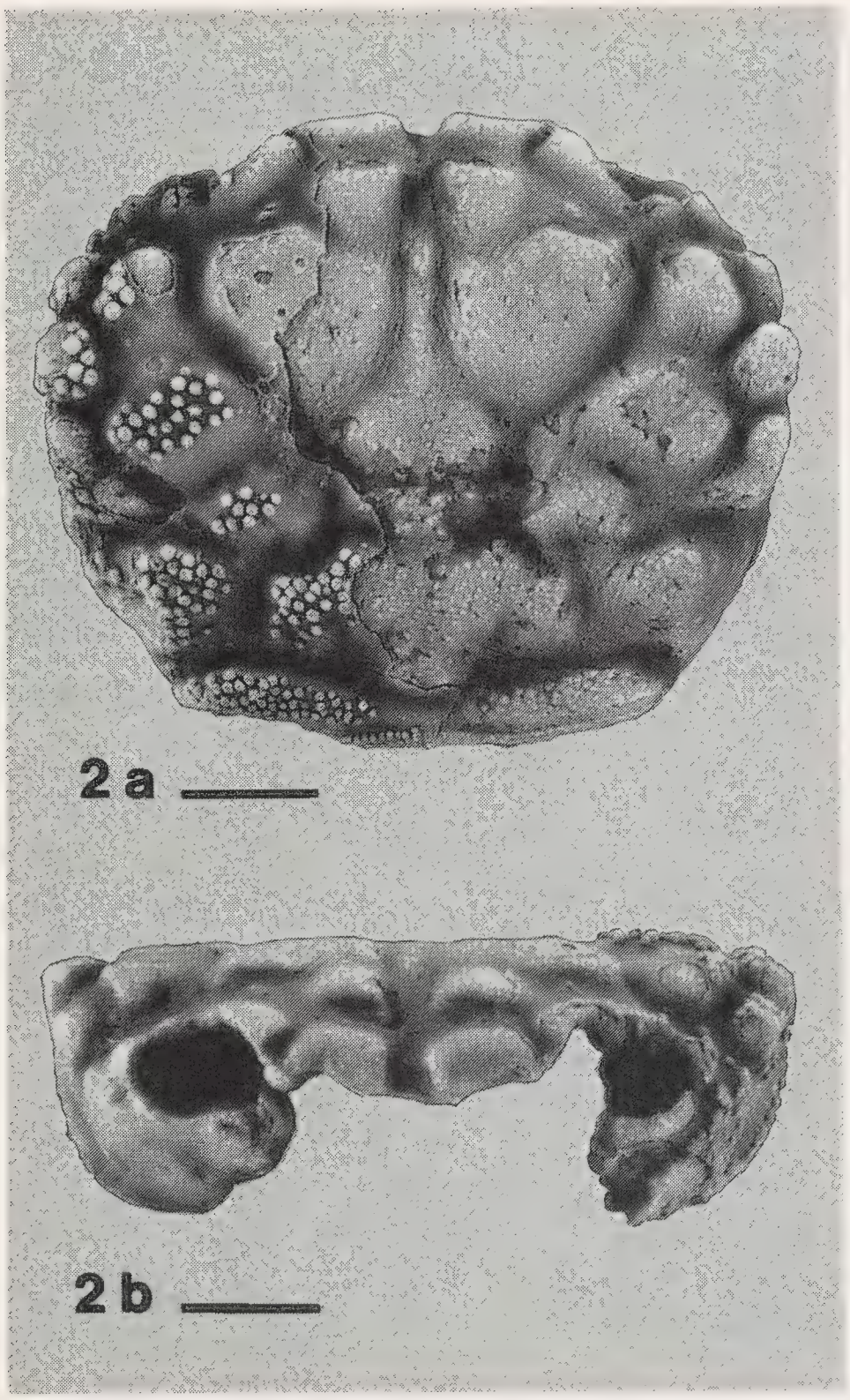
Type species: Eohalimede walleri Blow and Manning, 1996, p. 22, by original designation.

EOHALIMEDE SAUNDERSI, new species
Text-figure 2

Eohalimede walleri Blow and Manning, 1996, p. 22, paratype only (USNM 484581).

Diagnosis: Very similar to *Eohalimede walleri* in carapace outline, placement of prominences, and general character, but without mushroom-shaped prominences. In contrast to the mushroom-shaped prominences of *E. walleri,* the elevated surfaces of this new species are covered with clusters of tubercles.

Description: Carapace suboctagonal, width greater than length, broadest at second lateral tooth; regions well defined, distinctly elevated, apex of most with distinctive clusters of small



Text-figure 2. *Eohalimede saundersi* Blow and Manning n. sp. (2a.) Holotype, carapace in dorsal view, (ChM No. PI 15210), cl 9.5 mm, cw 11.0 mm. Scale = 2 mm. (2b.) Holotype above, carapace in anterior view. Scale = 2 mm.

Locality: M.M. Orangeburg Quarry, Orangeburg Co., South Carolina. Santee Limestone.

tubercles, surfaces of carapace though very finely punctate, appearing smooth to unaided eye.

Fronto-orbital width about 3/4 carapace width.

Front weakly projecting, bilobed, with deep, wide, median incision, width about 1/3 carapace width; lobes weakly divergent, truncate, thickened anteriorly, lower margins beaded.

Orbit oval (length 1 1/3 height), about half width of front, not produced beyond margin of carapace, composed of four unequal lobes, each decorated marginally with small, low, tubercles. Inner orbital lobe swollen, length slightly longer than middle and outer orbital lobes combined, separated from middle lobe by distinctive, deep fissure. Middle lobe subacute, projecting just beyond slightly larger, blunt, outer orbital lobe, separated from latter by shallow, narrow fissure. Suborbital lobe longer than inner orbital lobe, separated from outer orbital lobe by shallow fissure.

Anterolateral margin with 3 equally spaced, densely tuberculate, blunt prominences (or rounded teeth); first and second round, third elongate; first distinctly smaller than second and slightly smaller than third, set well behind orbit, flanked mesially by broader, elongate, hepatic cluster of tubercles; second and particularly third flanked mesially by large subrectangular epibranchial cluster of tubercles.

Posterolateral margin with a large, broadly triangular, raised prominence of clustered tubercles boarded laterally by deep grooves; outer or lower flank of prominence broadest, flattened; inner or upper surface of prominence narrowing while extending onto mesobranchial region, where highest.

Posterior border slightly concave at midline, width about one-third carapace width, margin defined by finely beaded rim.

Dorsal surface, exclusive of postfrontal and epigastric regions, regularly ornamented with about 17 clusters of low, peg-like tubercles; superior surfaces of tubercles round, smooth; surfaces between tubercle clusters, broad, smooth.

Postfrontal region narrow, deep, outermost surface lacking, without tubercles, apparently smooth.

Epigastric region very inflated anteriorly where truncated and highest, surfaces without tubercles, smooth.

Protogastric region broadly subcircular, not subdivided into lobes, surface with about 15 scattered tubercles; tubercles appear largest and most concentrated along anterolateral margin.

Mesogastric region broad basally, low, covered with tubercles; anterior extension slender, low, with three tubercles, one posterior and two near anterior end where extension separates epigastric lobes basally.

Urogastric region low, very narrow, ridge-like; surface defined by transverse row of 7 to 8 small tubercles; row separated from base of mesogastric region by narrow shallow groove marked by distinct, close set, slit-like, posterior gastric pits.

Cardiac region T-shaped; cross of T with 2

relatively small, submedian, elongate, tubercle clusters, each paired with slightly smaller, subcircular, metabranchial tubercle cluster; base of T a single, much smaller, oval cluster of tubercles.

Intestinal region low, smooth, bordered laterally on metabranchial region by narrow, elongate cluster of 50 or more low tubercles; cluster rising, widening and becoming more dense laterally.

Branchial region uneven, subregions distinct, elevated and separated by shallow, smooth, grooves.

Epibranchial region with largest tubercle cluster, subrectangular in shape, obliquely directed inward, anteriorly converging; cluster set near outer angle of protogastric lobe and separated from same by cervical groove.

Mesobranchial region with two tubercle clusters, the first, a central, single small cluster set near the submesial angle with the urogastric lobe and the second, a much larger cluster extending from the posterolateral margin.

Metabranchial region defined by prominent, elongate, transversely placed tubercle cluster near the posterolateral angle and a single much smaller subcircular cluster adjacent to the cardiac lobe.

Description based on complete dorsal aspect of carapace with much of the cuticle intact.

Etymology: This species is named for Albert E. Saunders of The Charleston Museum, in recognition of his contribution to South Carolina paleontology and in grateful appreciation for his years of support for the first author's research.

Holotype: Carapace (ChM No. PI 15210) cl 9.5 mm, cw 11.0 mm.

Type Locality: M.M. Orangeburg Quarry, Orangeburg Co., South Carolina. Santee Limestone.

Paratypes: Incomplete internal mold, without surface detail, of carapace with remnant of base of front present and the left lateral margin lacking (USNM 484581) cl (incomplete) 12.1 mm, cw (incomplete) 11.9 mm; locality USGS 26882 M.M. Berkeley Quarry, Berkeley County, South Carolina. Santee Limestone.

Incomplete carapace, remnant of left orbit present, right orbit and right anterolateral margin lacking (ChM No. PI 15200) cl 12.3 mm, cw 13.7 mm (incomplete), estimated cw 14.4 mm; M.M. quarry SE of Jamestown, Berkeley Co., South Carolina. Santee Limestone.

Occurrence: Santee Limestone, South Carolina.

Remarks: Those regions with elevated tubercle clusters appear highest and more coarsely tuberculate anteriorly with each sloping posteriorly, suggesting that these short ridges, like the much longer ridges found in *Lophoranina* (see Savazzi, 1981), might have aided this species in back burrowing.

Only three specimens of this species are thus far known to us.

V. LOCALITY DATA

M.M. Georgetown (= Jamestown) quarry, approx. 2.8 miles (4.5 km) N 33°E of Jamestown, on W side U.S. 17A, Georgetown Co., South Carolina.

M.M. Berkeley (= Cross) quarry, approx. 5.3 miles (8.5 km) SE of Eutawville, and about 2.2 miles (3.5 km) S 20°E of South Carolina Rtes. 6 and 45 intersection with secondary hwy 59 (Berkeley-Orangeburg Co. line road) on E side of secondary hwy 59, Berkeley Co., South Carolina.

M.M. quarry, S side South Carolina Rte. 45, 4.2 miles SE of South Carolina Rtes. 45 and 41 intersection in Jamestown, Berkeley Co., South Carolina .

M.M. Orangeburg quarry, W side South Carolina Rte. 59, 5.7 miles N of South Carolina Rte. 311, Orangeburg Co., South Carolina.

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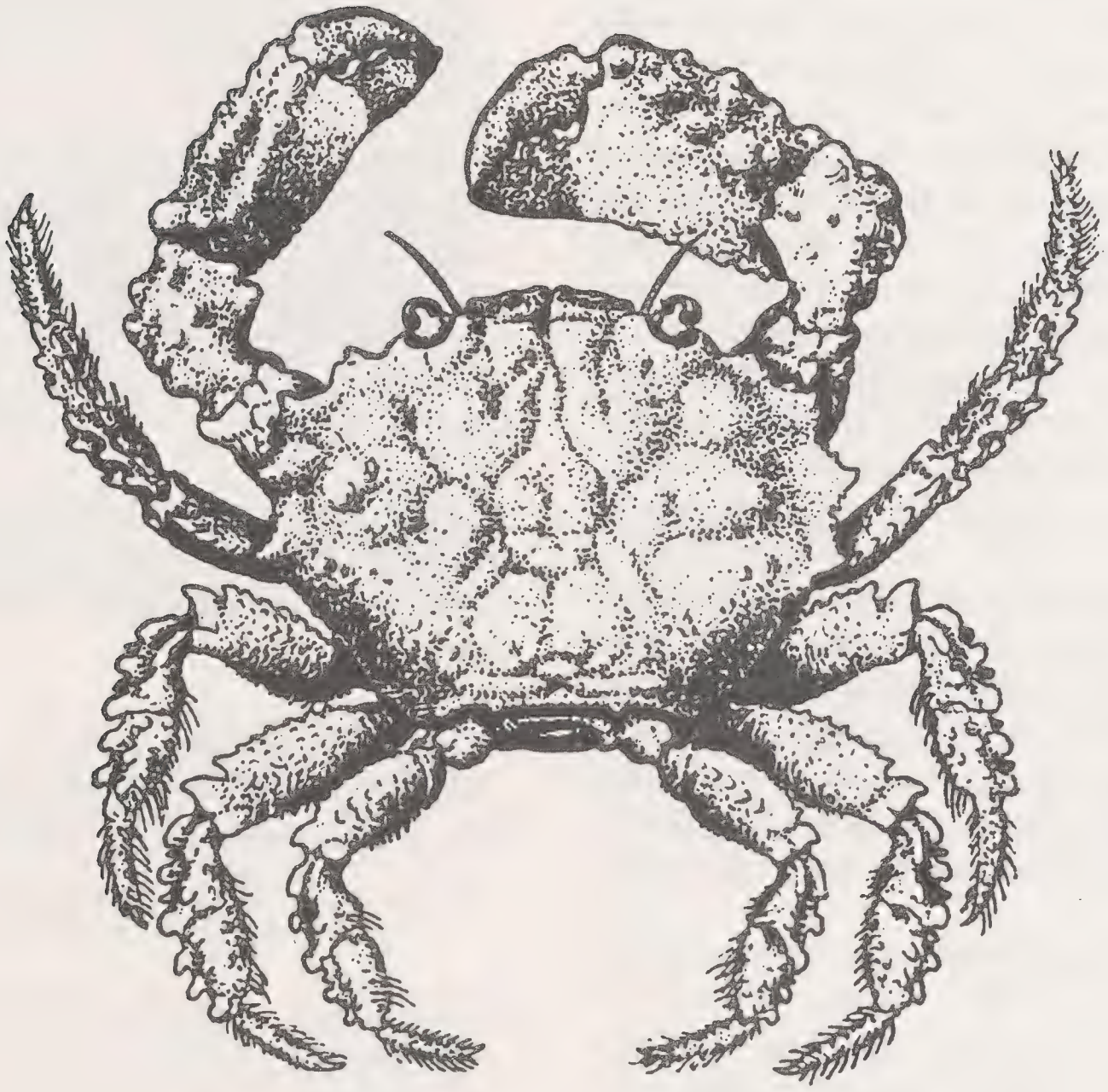

SUPERFAMILY MILIOLACEA: A THREE-FOLD LAYERED WALL --- SUPERFAMILY MILIOLACEA EHRENBERG, 1839, EMENDED; NEW SUPERFAMILY HAUERINACEA

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I. ABSTRACT

The Superfamily Miliolacea Ehrenberg, 1839, is here restricted to the calcareous imperforate Foraminiferida that have a pitted exterior surface and a wall composed of three layers. Excluded are those Foraminiferida that have a smooth porcelaneous surface, as exhibited when viewed in reflected light.

Described herein as new are the genera *Hemimiliola, Heteromiliola,* and *Miliolacostata*. These three genera are distinguished by the texture of the outer wall of the test (smooth, ribbed, or costate), the chamber arrangement, and the distribution of pits (juxtaposed or separated). Five new subfamilies are here designated and described: the HEMIMILIOLINAE, HETEROMILIOLINAE, TEXININAE, HELENTAPPANELLINAE, and MILIOLACOSTATINAE, which include all of the known species of Miliolacea from the Gulf Coastal Plain.

The new Superfamily HAUERINACEA, here designated, is erected to accommodate all former species of Miliolacea with a smooth porcelaneous surface, as exhibited when viewed in reflected light.

II. INTRODUCTION

The layered structure in the wall of *Miliola* was brought to my attention by Earl Manning, then a graduate student at Louisiana State University, who was studying a foraminiferal assemblage from the Pacific Ocean. He recovered and photographed a specimen of *Miliola* he identified as "*Quinqueloculina semireticulosa* Cushman" (Figure 2). His photomicrograph revealed a three-fold wall structure, the outer a thin layer of tabular calcite with microscopic punctations that also lines the wall and bottom of the pits (Figures 3, 5). Between the pits, the outer layer can be seen to overlie an unconsolidated aggregate of rodlike structures or crystals that are randomly oriented and held in place by the inner lining or "ceiling" of the chambers. Further, a photomicrograph of "*Quinqueloculina tuberculata* Cushman and Todd" [= *Hemimiliola jacksonensis* Cushman] displays the same three-fold arrangement of calcite layers in the wall of the test (see Figure 4). Other photomicrographs reveal pores at the base of the pits in the genera *Miliola* and *Hemimiliola.*

Loeblich and Tappan, in describing the Suborder Miliolina Delage and Hérouard, 1896, state:

> "Test of porcelaneous high magnesium calcite, of fine randomly oriented rodlike crystals, 1.5 µm to 2.0 µm in length and 0.24 µm in diameter, seen only with the electron microscope, the random crystal orientation refracting light in all directions to result in the milky opacity or porcelaneous appearance in reflected light, wall appears brown and glassy in transmitted light, may have surface layer of variously arranged tabular rhombohedral crystals, commonly with organic lining and may have added adventitious material; true pores may occur in protoconch of some, generally imperforate in post embryonic stage, but may have pseudopores..." [see Loeblich and Tappan 1988, p. 309]

Evidently, these "randomly oriented rodlike crystals" are the elements observed in the *middle layer* in the wall of *Miliola* and its relatives and the "surface layer of variously arranged tabular rhombohedral crystals" describes the outer layer in the wall of *Miliola*. Tests with tabular crystals in the outer layer of the wall do not exhibit a porcelaneous appearance. Why, then, did Loeblich and Tappan describe the entire Suborder Miliolina Delage and Hérouard, 1896, as "Test of porcelaneous high magnesium calcite..." ?

In their remarks following the description of the Family Hauerinidae Schwager, 1876, Loeblich and Tappan (1988, p. 332) state: "The Miliolidae are recognized as a

separate family, characterized by the numerous perforations or pseudopores in the wall." Pseudopores are defined (*ibid.*, p. 739) as "Deep pits in the surface of some Miliolacea that do not completely penetrate the wall, as in *Miliola*; punctations." These pseudopores occur between the pits; however, at the base of the pits they penetrate the wall, becoming true pores.

This writer considers the characterization of the Miliolidae by Loeblich and Tappan in their remarks on the Hauerinidae as both revealing and noteworthy. The most important visible feature of the entire family Miliolidae is the pitted exterior wall of the tests. This characteristic, with the three-fold layered structure of the wall, is sufficient to restrict the Superfamily Miliolacea Ehrenberg, 1839, to the pitted wall genera as characterized by the genotype species *Miliolites saxorum* Lamarck, 1804 [= *Miliola saxorum* (Lamarck), 1804].

Taxonomic Note: In 1986, Loeblich and Tappan restricted the genus *Dentalina* to "those species with longitudinally costate surface" (quoted in 1988, p. 395) and erected *Laevidentalina* for those species "very finely perforate" with "surface smooth and unornamented" (see 1988, p. 396), illustrating the wall of a specimen from the Gulf of Mexico, SEM X7000 (pl. 439, fig. 24). This writer decided to investigate whether additional homogeny in the Miliolacea of the Gulf Coastal Plain would appear if costate miliolid species were separated from those with smooth surfaces. The result of this investigation is presented in Table I.

III. SYSTEMATIC DESCRIPTIONS AND EMENDATIONS

Superfamily MILIOLACEA Ehrenberg, 1839

Emended Diagnosis: Test free, coiled; outer wall with punctations; pits juxtaposed or irregularly dispersed; surface of test smooth, ribbed or costate; proloculus followed by coiled chambers, two per volution; wall of test consisting of three layers of calcite: a tabular layer of granular calcite that contains punctations, which overlies a mass of loosely stacked, randomly oriented calcite rods lying on the calcareous imperforate inner wall of the chamber; base of pits with pores; aperture terminal with or without trematophore on orifice. Eocene to Holocene.

Family MILIOLIDAE Ehrenberg, 1839

Emended Diagnosis: Test with chambers one-half coil in length added in one or more numerous planes; *wall smooth, ribbed or with costae.* Eocene to Holocene (cf. Loeblich and Tappan, 1988, p. 352).

Subfamily MILIOLINAE Ehrenberg, 1839

Emended Diagnosis: Test wall smooth, pits aligned or randomly disposed, elongate oval, proloculus followed by chambers one-half coil in length added in different planes. Eocene to Holocene. (cf. Loeblich and Tappan, 1988, p. 353).

Genus MILIOLA Lamarck, 1804

Type species: *Miliolites saxorum* Lamarck, 1804.

Emended Diagnosis: Test narrow and elongate fusiform; chambers one-half coil in length, quinqueloculine, with separate floor; wall calcareous, *pitted, three-layered with a tabular surface layer bearing perforations or "pits," a middle layer of randomly oriented calcite rods, and an inner lining or "ceiling;"* surface of test may have longitudinal costae *or ribs*; aperture terminal on ultimate chamber with trematophore. [Emendation to diagnosis of Miliola by Loeblich and Tappan, 1988, p. 353.]

MILIOLA SAXORUM (Lamarck)
Figures 12-14

Miliolites saxorum LAMARCK, 1804, Annales Mus. Hist. Nat., vol. 5, p. 352.

Quinqueloculina saxorum (Lamarck). D'ORBIGNY, 1826, Ann. Sci. Nat., vol. 7, p. 301, no. 1, pl. 16, figs. 9-14.

Miliola saxorum (Lamarck). CUSHMAN, 1935, U. S. Geol. Surv., Prof. Paper 181, p. 12, pl. 3, figs. 1-3; BERGQUIST, 1942, Mississippi Geol. Surv., Bull. 49, p. 25, pl. 2, fig. 8; CUSHMAN and TODD, 1945, Cushman Lab. Foram. Res., Contr., vol. 21, pt. 4, p. 83; ANDERSEN, 1984, Tulane Stud. Geol. Paleont., vol. 18, no. 1, p. 5, figs. 5-16; ANDERSEN, 1988, Tulane Stud. Geol. Paleont.,

TABLE I

Wall and Chamber Arrangement of Pitted Miliolidae in the Gulf Coastal Plain

WALL	GENUS AND SPECIES	CHAMBERS
SMOOTH	Miliola alphillipsi Miliola chipolensis Miliola newberryensis Miliola saxorum	Quinqueloculine
	Hemimiliola jacksonensis	Quinqueloculine to Planispiral
	Neaguites byramensis * Neaguites inusitatus *	Planispiral
	Heteromiliola decorata **	
	Texina ferayi ***	
BROAD RIBS	Helentappanella punctatocostata	Quinqueloculine to Planispiral
COSTATE	Miliolacostata byramensis Miliolacostata jacksonensis Miliolacostata rolandi	Quinqueloculine
	Picouina mississippiensis	Triserial

* Pits juxtaposed.
** Outer wall white, granular calcite.
*** Pits not juxtaposed.

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vol. 21, no. 4, p. 130, figs. 17, 18.

Miliola cf. *M. saxorum* (Lamarck). ANDERSEN, 1988, Tulane Stud. Geol. Paleont., vol. 21, no. 4, p. 132, fig. 19.

Emended Diagnosis: Test large, elongate, fusiform; chambers quinqueloculine, numerous, distinct and pitted; *wall three-fold with surface layer consisting of tabular, calcareous plates bearing perforations which extend into base of pits; middle layer consisting of a loose aggregate of calcite rods terminating at outer wall of pits;* aperture at end of a short neck with trematophore. Length 2.50 mm; breadth 0.69 mm.

Remarks: The distribution of the pits and the length-breadth ratio of *Miliola* cf. *M. saxorum*, from the Yazoo Formation, are comparable to the characteristic *Miliola saxorum* from the Moodys Branch Formation. However, the actual measurements of the former, 1.20 mm long and 0.34 mm wide, are much smaller than the latter, which is 2.50 mm in length and 0.69 mm in breadth. Both are mature specimens. The environments are different, which could account for the smaller size of the Red Bluff Formation specimen (see Environmental Implications below).

MILIOLA ALPHILLIPSI Andersen
Figures 6, 7

Miliola alphillipsi ANDERSEN, 1988, Tulane Stud. Geol. Paleont., vol. 21, no. 4, p. 136, fig. 28.

Emended Diagnosis: Test free, pitted, quinqueloculine chamber arrangement, slightly more than twice as long as wide, transverse section broadly triangular with periphery rounded; neck, *which extends above penultimate chamber, with surface covered by closely spaced costae randomly distributed at distal end;* pores present in each pit; *aperture simple.* Length of holotype: 0.49 mm; width 0.21 mm.

Remarks: All known specimens of this species were recovered from the type locality of the Byram Formation (Oligocene).

MILIOLA CHIPOLENSIS
(Cushman and Ponton)
Figures 8, 9

Quinqueloculina chipolensis CUSHMAN and PONTON, 1932, Florida Geol. Surv., Bull. 9, p. 45, figs. 1a, b, 2a, b, 3.

Miliola chipolensis (Cushman and Ponton) ANDERSEN, 1988, Tulane Stud. Geol. Paleont., vol. 21, no. 4, p. 132, figs. 22, 23.

Remarks: The description of this species was emended by Andersen in 1988.

MILIOLA NEWBERRYSENSIS (Puri)
Figures 10, 11

Quinqueloculina newberryensis PURI, 1957, Florida Geol. Surv., Bull. 38, p. 107, pl. 3, figs. 3a, b.

Miliola newberryensis (Puri). ANDERSEN, 1988, Tulane Stud. Geol. Paleont., vol. 21, no. 4, p. 134, fig. 26.

Remarks: This species is from the Crystal River Formation in Florida. All specimens recovered have weathered surfaces; however, rodlike calcite structures in the middle layer of the test were revealed with scanning electron microscope examination.

Subfamily HEMIMILIOLINAE Andersen,
new subfamily

Diagnosis: Wall smooth, pitted but with pits not juxtaposed; quinqueloculine, followed by chambers one-half coil in length added at 180°. Eocene, North America.

Genus HEMIMILIOLA Andersen,
new genus

Type species: *Massilina jacksonensis* Cushman, 1927.

Diagnosis: Wall smooth, pitted; quinqueloculine to planispiral; pores at base of pits; aperture on a short neck with trematophore; chambers rounded to carinate.

HEMIMILIOLA JACKSONENSIS (Cushman)
Figures 15-17

Massilina jacksonensis CUSHMAN, 1927, Journ. Paleontology, vol. l, p. 150, pl. 23, figs. 5, 6; CUSHMAN, 1935, U. S. Geol. Surv., Prof. Paper 181, p. 13, pl. 3, figs. 7-10; CUSHMAN and TODD, 1945, Cushman Lab. Foram. Res., Contr., vol. 21, pt. 4, p. 82, pl. 13, fig. 17.

Massilina cf. *jacksonensis,* PURI, 1957, Florida Geol. Surv., Bull. 38, p. 108, pl. 3, figs. 2a, b.

Quinqueloculina tuberculata CUSHMAN and TODD, 1945, Cushman Lab. Foram. Res., Contr., vol. 21, pt. 4, p. 81, pl. 13, figs. 11, 12.

Tappanella jacksonensis (Cushman). ANDERSEN, 1984, (non *Tappanella* Gudina and Saidova, 1969), Tulane Stud. Geol. Paleont., vol. 18, no. 1, p. 12, figs. 30-33.

Heterellina jacksonensis (Cushman). ANDERSEN, 1988, Tulane Stud. Geol. Paleont., vol. 21, no. 4, p. 138, fig. 32.

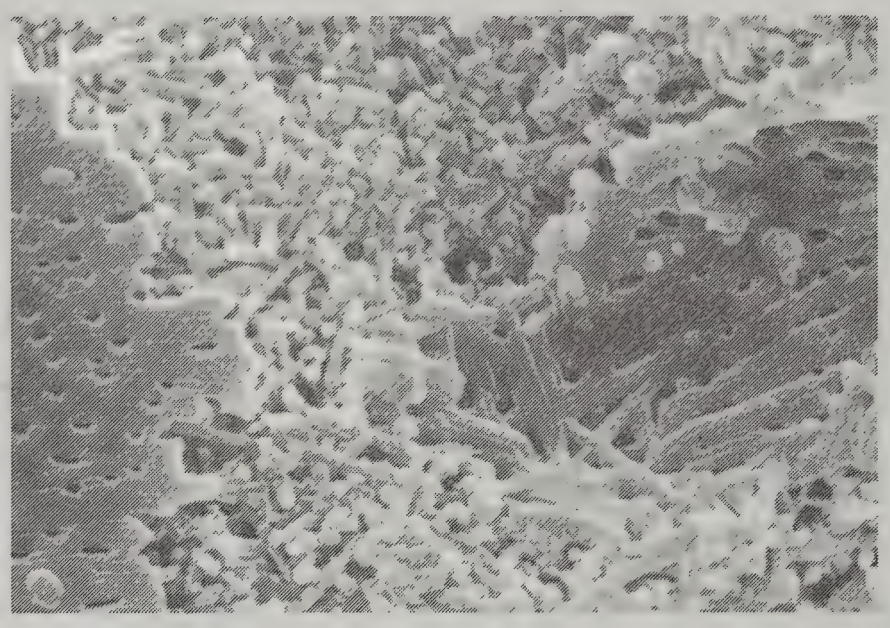
Emended Diagnosis: Test *free*, broadly oval or elliptical, compressed; chambers acute to slightly rounded, ultimate chamber extending slightly beyond penultimate chamber; pits randomly distributed over smooth chamber wall; early chambers quinqueloculine, later chambers added at 180° in a single plane; aperture on a short neck with trematophore. Length 1.40 mm; breadth 1.00 mm; thickness 0.20 mm.

Remarks: Figured specimens 15 and 17, LSU Geoscience Museum numbers 11548 and 11549, are from the Moodys Branch Formation in Jackson Park, Jackson, Mississippi. Four genera of the family Miliolidae are present in abundance at this locality (see Table II).

Subfamily NEAGUITESINAE
Andersen, 1984

Emended Diagnosis: Wall smooth, pitted with

1



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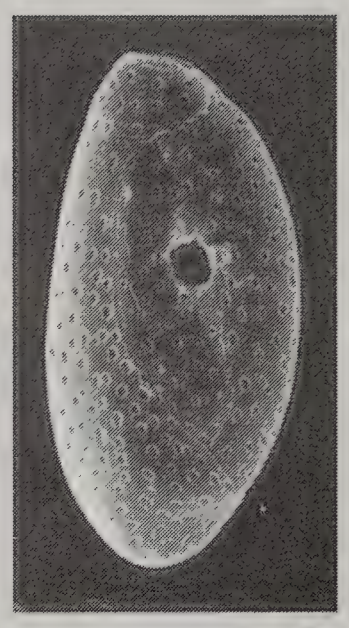

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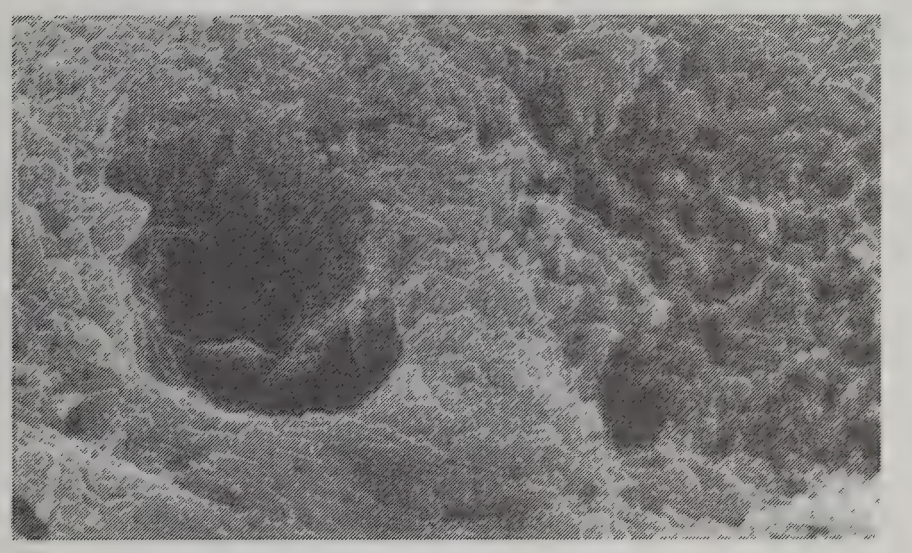

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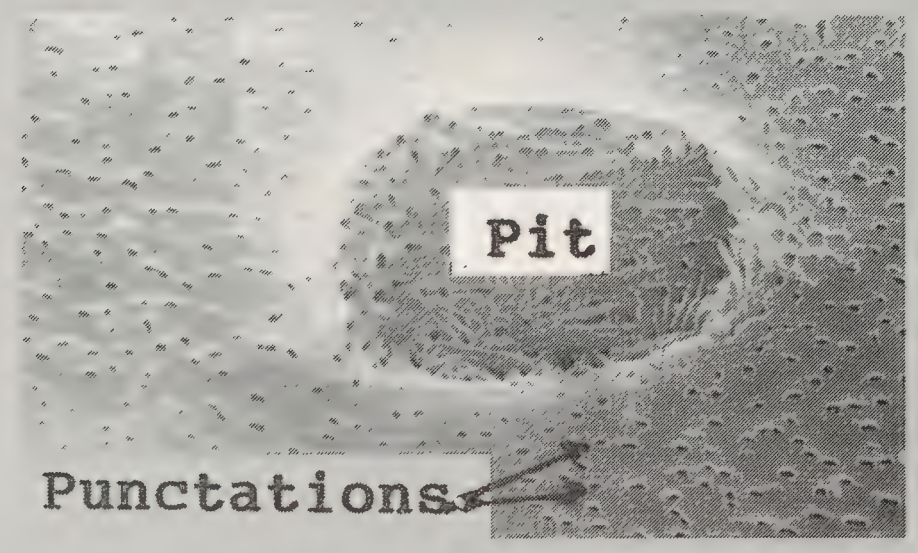

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Figures 1-5

1. "*Quinqueloculina tuberculata* Cushman and Todd"
   Weathered specimen X 75
2. "*Quinqueloculina semireticulosa* Cushman"
   Lateral view X 75
3. "*Quinqueloculina semireticulosa* Cushman"
   Section of wall showing layering X 3750
4. "*Quinqueloculina tuberculata* Cushman and Todd"
   View showing rod-like elements in middle layer X 2500
5. "*Quinqueloculina semireticulosa* Cushman"
   View identifying "pit" and "punctations" X 3750

pits juxtaposed; chambers planispirally coiled. Eocene and Oligocene, North America.

Genus NEAGUITES Andersen, 1984

Type species: *Spiroloculina byramensis* Cushman, 1922.

Emended Diagnosis: Test elliptical, sides flattened to slightly concave; *wall* pitted with pits juxtaposed; chamber arrangement consisting of two chambers per volution added at 180°; aperture terminal, simple.

Remarks: Removal of the outer wall in weathered specimens reveals the rodlike, calcite elements of the middle layer in the wall of the test (see Andersen, 1984, Figure 40). Weathered specimens also

reveal that pores are present in the bottom of each pit.

NEAGUITES BYRAMENSIS (Cushman)
Figures 18, 19

Spiroloculina byramensis CUSHMAN, 1922, U. S. Geol. Surv., Prof. Paper 129, p. 101, pl. 25, figs. 4a, b.

Neaguites byramensis (Cushman). ANDERSEN, 1984, Tulane Stud. Geol. Paleont., vol. 18, no. 1, p. 15, figs. 39, 40; ANDERSEN, 1988, Tulane Stud. Geol. Paleont., vol. 21, no. 4, p. 138, fig. 33.

Emended Diagnosis: Test compressed, elliptical *to nearly round; wall with pits juxtaposed to the extent that test is almost covered with adjoining pits;* proloculus and early chambers normally concealed; periphery rounded; *aperture simple* at end of a short neck. Figured specimen: length 9.55 mm; breadth 0.51 mm.

NEAGUITES INUSITATUS Andersen
Figures 20, 21

Neaguites inusitatus ANDERSEN, 1984, Tulane Stud. Geol. Paleont., vol. 18, no. 1, p. 15, figs. 37, 38.

Original Diagnosis: "Test small, elliptical in outline, twice as long as broad; flat, megalospheric form with visible proloculus followed by two chambers per volution added in a single plane, microspheric form with early chambers at an angle to the plane of coiling; periphery rounded to broadly acute; aperture end extends beyond the penultimate chamber, final chamber frequently forming an eyelet at the base of the test by not remaining in juxtaposition with the preceding chamber; chambers with a frosted appearance produced by its intensely pitted surface wherein there are perforations; aperture on a slight neck. Length of holotype 0.60 mm; breadth 0.30 mm." (Andersen, 1984)

Remarks: In this species, the pits are closely juxtaposed as in *Neaguites byramensis.*

Subfamily HETEROMILIOLINAE
Andersen, new subfamily

Diagnosis: Wall smooth, pitted; external portion of three-layered wall composed of white, granular calcite; chambers planispiral in arrangement. Eocene and Oligocene, North America.

Genus HETEROMILIOLA, new genus

Type species: *Massilina decorata* Cushman, 1922.

Diagnosis: Test free, flattened and elliptical; pits randomly distributed on the surface of test, not juxtaposed; outer wall composed of white, granular calcite; two chambers per volution, added at 180°; proloculus rarely visible on side of test; aperture simple.

HETEROMILIOLA DECORATA (Cushman)
Figures 22-24

Massilina decorata CUSHMAN, 1922, U. S. Geol. Surv., Prof. Paper 129-F, p. 143, pl. 34, fig. 7; CUSHMAN, 1935, U. S. Geol. Surv., Prof. Paper 181, p. 13, pl. 3, fig. 14.

Spiroloculina lamposa HUSSEY, 1949, Journ. Paleontology, vol. 23, no. 2, p. 121, pl. 26, fig. 6.

Neaguites lamposus (Hussey). ANDERSEN, 1984, Tulane Stud. Geol. Paleont., vol. 18, p. 16, figs. 41, 42.

Neaguites decoratus (Cushman). ANDERSEN, 1988, Tulane Stud. Geol. Paleont., vol. 21, no. 1, p. 138, figs. 35-38.

Original Diagnosis: "Test much flattened, elliptical or oval, slightly longer than wide, basal and apertural ends projecting, the apertural end narrowed to a small cylindrical neck, nearly in the longitudinal axis of the test; sutures rather indistinct; surface dull white; periphery rounded, the sides ornamented by very fine pits, giving a finely granular appearance to the test. Length 1 millimeter or less." (Cushman, 1922). In 1935, Cushman added that the finely granular surface gave the test a "matte appearance."

Remarks: Heteromiliola decorata is not admissible to any genus presently assigned to the Miliolidae. It satisfies the basic requirements of the family because the test wall is composed of three layers and is pitted (see Andersen, 1988, Figure 36). However, the pits are not juxtaposed (Andersen, 1988, Figure 38), thus this species cannot be placed in the genus *Neaguites.*

All of the other smooth-walled genera in the Miliolacea appear to have an outer test wall similar to the Holocene genus *Miliola,* as demonstrated by Earl Manning (see Introduction, above). In Figures 22 and 23 (herein), it can be noted that the

outer layer of the wall of *Heteromiliola decorata* consists of interlocked, elongate, flat sheets of calcite with numerous perforations. The granular, outer wall of this species, therefore, is unique to the Miliolidae. In addition, the pits as seen on weathered specimens appear as "reel-shaped" elements. Coccolith plates are commonly present among the debris adhering to the wall of the test.

Tests of *Heteromiliola decorata,* examined and analyzed with an X-ray diffraction unit by Professor Ray E. Ferrell, Jr., Louisiana State University, are composed of calcite, negating the possibility that *Heteromiliola* is related to the porcelaneous Foraminiferida, which are composed of aragonite. This difference in composition could explain the fact that the surfaces of all recovered tests of this genus are strongly weathered.

Subfamily TEXININAE Andersen, new subfamily

Diagnosis: Wall pitted, but pits not juxtaposed, planispirally coiled, aperture terminal with trematophore. Eocene, North America.

Genus TEXINA Andersen, 1984

Type species: *Texina ferayi* Andersen, 1984.

Emended Diagnosis: Test free, pitted with pits not juxtaposed, sides flattened, periphery rounded; wall three-layered with rods in middle layer exposed on the surface of the wall; planispirally coiled with two chambers per volution; aperture with trematophore.

TEXINA FERAYI Andersen
Figures 25-27

Spiroloculina smithvillensis FERAY, 1948, Dissertation, University of Wisconsin, 1948 *[nomen nudum].*

Texina ferayi ANDERSEN, 1984, Tulane Stud. Geol. Paleont., vol. 18, no. 1, p. 17, figs. 43-46.

Neaguites ferayi (Andersen). LOEBLICH and TAPPAN, 1988, Foraminiferal Genera and Their Classification: Van Nostrand Reinhold Co., Inc., vol. 1, p. 352, pl. 360, figs. 12-15.

Emended Diagnosis: Test planispiral, nearly round in outline, compressed; apertural end nearly flush with periphery; pits randomly distributed over unornamented chambers; *white spots appearing on outer wall between pits are ends of calcite rods in middle layer of test;* aperture at end of a short neck, with trematophore. Length of holotype: 0.48 mm; breadth 0.45 mm.

Remarks: A taxonomic mistake occurred when the genus *Texina* was described in 1984, four years before the discovery of the three-fold arrangement of the calcite in the walls of the Miliolacea. Loeblich and Tappan (1988, p. 352-353) placed *Texina* in synonymy with *Neaguites* because the "possible inclusions in the wall of *Texina*" might be the "result of secondary overgrowth due to diagenesis rather than an intrinsic part of the test structure." These "possible inclusions," appearing as round, white spots on the test wall, actually are the ends of calcite rods in the middle layer of the wall and, thus, are an intrinsic part of the structure of the test. These "spots" occur also in the wall of *Helentappanella punctatocostata* (Cushman) from the Moodys Branch Formation (see Figure 30), and *Miliola saxorum* (Lamarck) from Damery, France (see Figure 14).

Loeblich and Tappan, in their remarks on the genus *Texina*, state "*Neaguites* was described as having a simple aperture and *Texina* as having a cribrate one. However, the last chamber of the holotype is broken, hence the apertural characters are not shown in the original figures." (1988, p. 353). The first feature destroyed, when such a specimen is subjected to wear or weathering, commonly is the cribrate aperture. The holotype (Andersen, 1984, fig. 43) was selected for the well-preserved chambers. The paratype (*ibid.*, Figure 44), with a partially preserved aperture, reveals that *Texina* does have a cribrate aperture (see Figure 27 herein).

Subfamily HELENTAPPANELLINAE Andersen, new subfamily

Diagnosis: Wall ribbed with pits on ribs and in valleys between ribs; early chambers quinqueloculine, later added at 180°; aperture with trematophore. Eocene, North America.

Genus HELENTAPPANELLA Andersen, 1985

Type species: *Massilina jacksonensis* Cushman var. *punctatocostata* Cushman, 1933.

Emended Diagnosis: Test free, pitted, early chambers quinqueloculine, later chambers added at 180°, elliptical, compressed; periphery angular or rounded; wall three-layered with broad, pitted ribs.

HELENTAPPANELLA PUNCTATOCOSTATA
(Cushman)
Figures 28-30

Massilina jacksonensis Cushman var. *punctatocostata* CUSHMAN, 1933, Cushman Lab. Foram. Res., Contr., vol. 9, pt. 1, p. 3, figs. 5, 6.

Tappanella punctatocostata (Cushman). ANDERSEN, 1984, Tulane Stud. Geol. Paleont., vol. 18, no. 1, p. 12, figs. 26-29.

Helentappanella punctatocostata (Cushman). ANDERSEN, 1985, Micropaleontology, vol. 31, p. 67 [new name for *Tappanella* Andersen *non* Gudina and Saidova, 1969.

Emended Diagnosis: Test broadly elliptical to nearly round, much compressed, periphery ranging from acute to slightly rounded depending on position of *pitted ribs* relative to periphery; apertural end extending slightly beyond penultimate chamber; early chambers quinqueloculine, later ones added at 180° in a single plane; surface ornamented with low, flat, *wide ribs* oriented either parallel to long axis of chamber or cutting diagonally across chamber; sutures difficult to discern because of *ribs;* aperture with trematophore at end of a short neck. Length of figured specimen: 2.95 mm; breadth 2.05 mm.

Subfamily MILIOLACOSTATINAE Andersen, new subfamily

Diagnosis: Wall pitted, costate; pits aligned between acute costae; aperture simple. Eocene and Oligocene, North America.

Genus MILIOLIACOSTATA, new genus

Type species: *Miliola jacksonensis* Cushman, 1933.

Diagnosis: Wall with longitudinal costae, pits juxtaposed in valleys between costae; quinqueloculine chamber arrangement; test fusiform with base rounded; aperture terminal, simple, and elevated on a short neck which extends above penultimate chamber.

MILIOLACOSTATA JACKSONENSIS (Cushman)
Figures 33, 34

Miliola jacksonensis CUSHMAN, 1933, Cushman Lab. Foram. Res., Contr., vol. 9, pt. l, p. 2, pl. 1, figs. 2, 3; CUSHMAN, 1935, U. S. Geol. Surv., Prof. Paper 181, p. 13, pl. 3, figs. 4-6; CUSHMAN and TODD, 1945, Cushman Lab. Foram. Res., Contr., vol. 21, pt. 4, p. 83, pl. l3, fig. 13; BANDY, 1949, Bull. Amer. Paleontology, vol. 32, no. 131, p. 22, pl. 2, figs.

Figures 6-17

Subfamily MILIOLINAE Ehrenberg, 1839

Miliola alphillipsi Andersen
6. Lateral view X 50
7. Enlargement of pits X 1000

Miliola chipolensis (Cushman and Ponton)
8. Lateral view X 75
9. Enlargement of pits X 1000

Miliola newberryensis (Puri)
10. Lateral view X 50
11. Enlargement of pits X 1000

Miliola saxorum (Lamarck)
12. Lateral view X 33
13. Enlargement of pits X 1000
14. Calcite rods from middle layer of wall exposed on surface of the test X 2000

Subfamily HEMIMILIOLINAE Andersen, new subfamily

Hemimiliola jacksonensis (Cushman)
15. Lateral view X 25
16. Enlargement of pits X 1500
17. Lateral view of carinate form X 25

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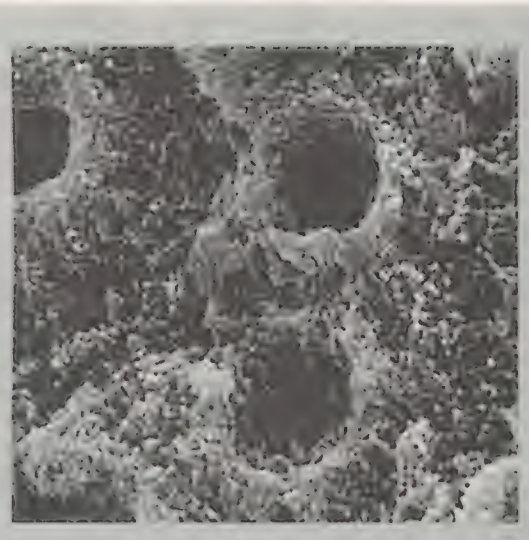

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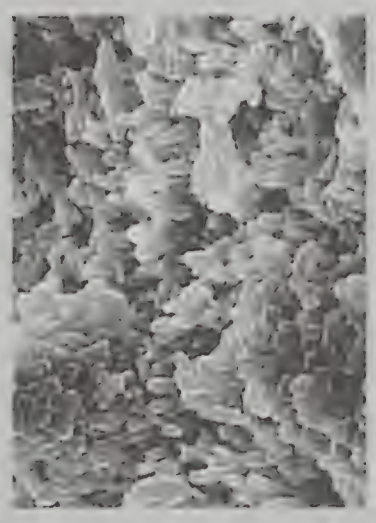

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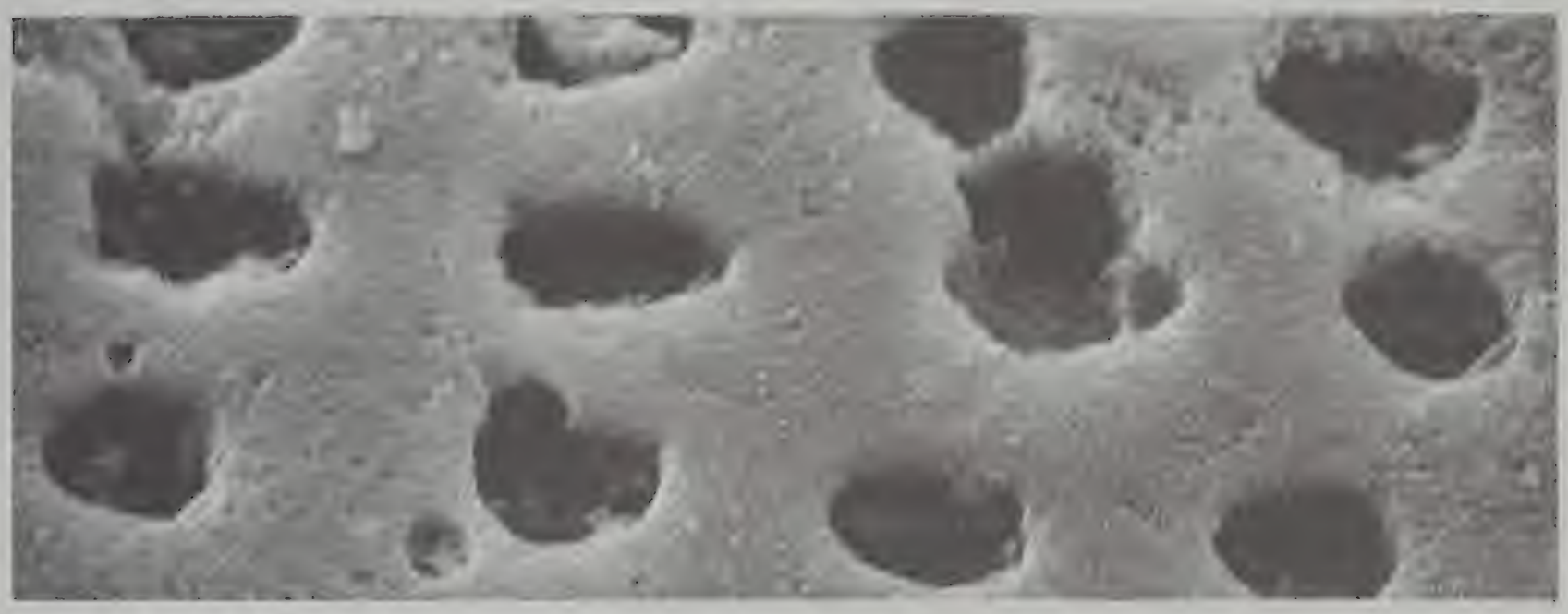

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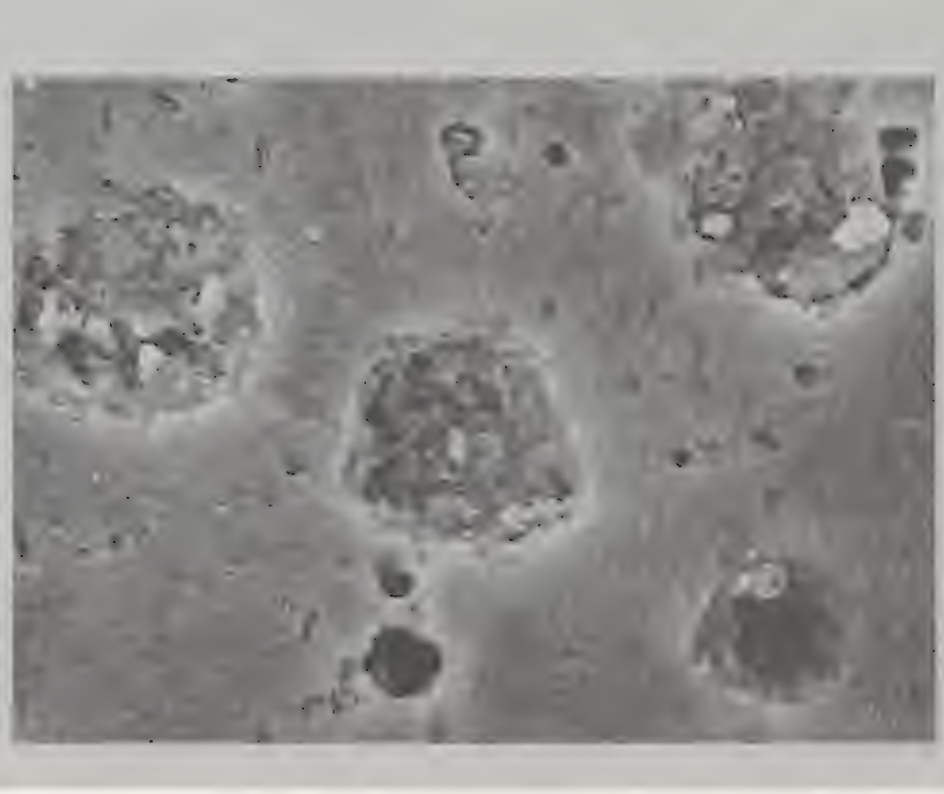

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Figures 6-17

6a-c; ANDERSEN, 1984, Tulane Stud. Geol. Paleont., vol. 18, no. 1, p. 5, figs. 17-19.

Miliola cf. *M. jacksonensis* FRANKLIN, 1944, Journ. Paleontology, vol. 18, pl. 45, fig. 6; ANDERSEN, 1988, Tulane Stud. Geol. Paleont., vol. 21, no. 4, p. 134, fig. 25.

Emended Diagnosis: Test large, *elongate,* fusiform, *quinqueloculine chamber arrangement;* chambers numerous, distinct, pitted; *base of pits with one or more pores; acute costae with uniformly spaced transverse ridges that separate juxtaposed pits between costae;* aperture at end of a very short neck, cribrate. Length 2.00 mm; breadth 0.55 mm.

MILIOLACOSTATA BYRAMENSIS (Cushman)

Figures 31, 32

Quinqueloculina byramensis CUSHMAN, 1923, U. S. Geol. Surv., Prof. Paper 133, p. 54, pl. 8, fig. 3.

Miliola byramensis (Cushman). ANDERSEN, 1984, Tulane Stud. Geol. Paleont., vol. 18, no. 1, p. 8, figs. 20-22.

Emended Diagnosis: Test quinqueloculine, approximately twice as long as broad, final chamber projecting slightly beyond penultimate chamber at both ends of test; *wall with acute* elevated costae longitudinally disposed; *pits forming a single line in valley between costae with eyelets in costae occupying space between pores;* aperture simple, on a short neck. Length 0.3 mm to 0.4 mm.

MILIOLACOSTATA ROLANDI (Andersen)

Figures 35, 36

Miliola rolandi ANDERSEN, 1984, Tulane Stud. Geol. Paleont., vol. 18, no. 1, p. 8, figs. 24, 25.

Emended Diagnosis: Test small, *costate*, elongate, approximately 2.5 times as long as broad, quinqueloculine; base rounded, final chamber extending above penultimate chamber; periphery rounded; *single row of pits in each valley between costae with each pit occupying position of space between pits in the adjacent valley;* aperture simple, at end of a very short neck. Length of figured specimen: 0.54 mm; breadth 0.20 mm.

Genus PICOUINA Andersen, 1984

Type species: *Triloculina mississippiensis* Cushman, 1935.

Original Diagnosis: "Test free, triloculine chamber arrangement; wall calcareous perforate; chambers with a series of pits with single perforation extending into the chamber; aperture cribrate." (Andersen, 1984)

PICOUINA MISSISSIPPIENSIS (Cushman)

Figures 37, 38

Triloculina mississippiensis CUSHMAN, 1935, Cushman Lab. Foram. Res., Contr., vol. 11, pt. 2, p. 25.

Picouina mississippiensis (Cushman). ANDER-

Figures 18-27

Subfamily NEAGUITINAE Andersen, 1984

Neaguites byramensis (Cushman)

18. Lateral view X 113
19. Enlargement of pits X 1000

Neaguites inusitatus Andersen

20. Lateral view X 150
21. Enlargement of pits X 1000

Heteromiliola decorata (Cushman)

22. Lateral view X 50
23. Enlargement of wall showing "reel-shaped" structures and adherent coccoliths X 1000
24. Enlargement showing the rodlike structures or crystals in the middle layer of test wall X 3750

Subfamily TEXININAE Andersen, new subfamily

Texina ferayi Andersen

25. Lateral view X 125
26. Enlargement of pits X 1000
27. Apertural view of paratype showing residual segment of cribrate aperture X 225

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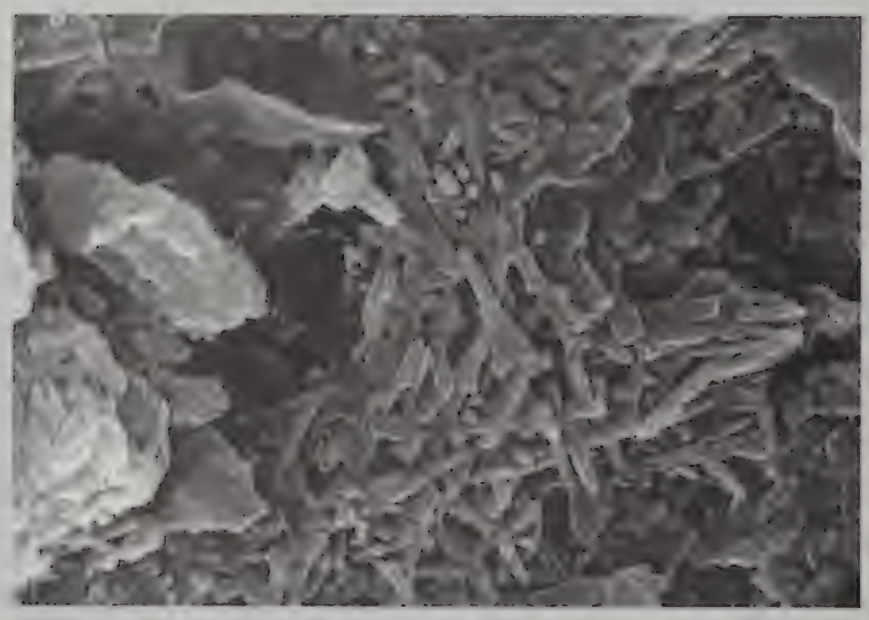
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Figures 18-27

SEN, 1984, Tulane Stud. Geol. Paleont., vol. 18, no. 1, p. 14, figs. 34, 35.

Original Diagnosis: "Test elongate, fusiform, broadly rounded in end view, both ends of the chambers extending well beyond the previous ones; chambers fairly distinct, very elongate, semicircular in transverse section, periphery broadly rounded; sutures rather indistinct; wall ornamented with numerous, 10-12, longitudinal costae running the entire length of the chamber, with fine rectangular pits in the grooves between the costae, of uniform size and regular position; aperture small, nearly circular, with a slight, rounded lip. Length 0.60-0.65 mm; breadth 0.15 mm; thickness 0.12 mm." (Cushman, 1935)

Emended Diagnosis: "Test calcareous, perforate, small, elongate, triloculine; periphery broadly rounded; chambers fairly distinct, interior simple, semicircular in transverse section; final chamber extending well beyond the penultimate chamber, apertural end pointed; wall ornamented with numerous longitudinal costae extending the entire length of the chamber, very fine, circular, uniform sized pits in grooves between costae; sutures indistinct due to the costate ornamentation; aperture cribrate." (Andersen, 1984). Figured specimen: Length 0.60-0.65 mm; breadth 0.15 mm; thickness 0.15 mm.

Remarks: The holotype of *Triloculina mississippiensis* Cushman, as described and figured in 1935, has an "aperture small, nearly circular, with a slight, rounded lip." Our figured specimen of *Picouina mississippiensis* (Cushman) exhibits a cribrate aperture; thus, our specimen does not agree with Cushman's interpretation of this species.

IV. NEW SUPERFAMILY

Superfamily HAUERINACEA Andersen, new superfamily

Diagnosis: Wall calcareous, porcelaneous in reflected light; test coiled, with two or more chambers per volution in varying planes about the longitudinal axis, may become involute or may uncoil; some forms may have secondary partitions within the chambers; aperture with trematophore or simple. Upper Triassic to Holocene.

Remarks: The emendation of the Superfamily Miliolacea [see above] to include only those forms with punctations and pores within the wall structure makes necessary the establishment of a new superfamily to accommodate those forms formerly included in the Superfamily Miliolacea which have a calcareous porcelaneous wall and lack perforations or pores. Thus, this division will eliminate

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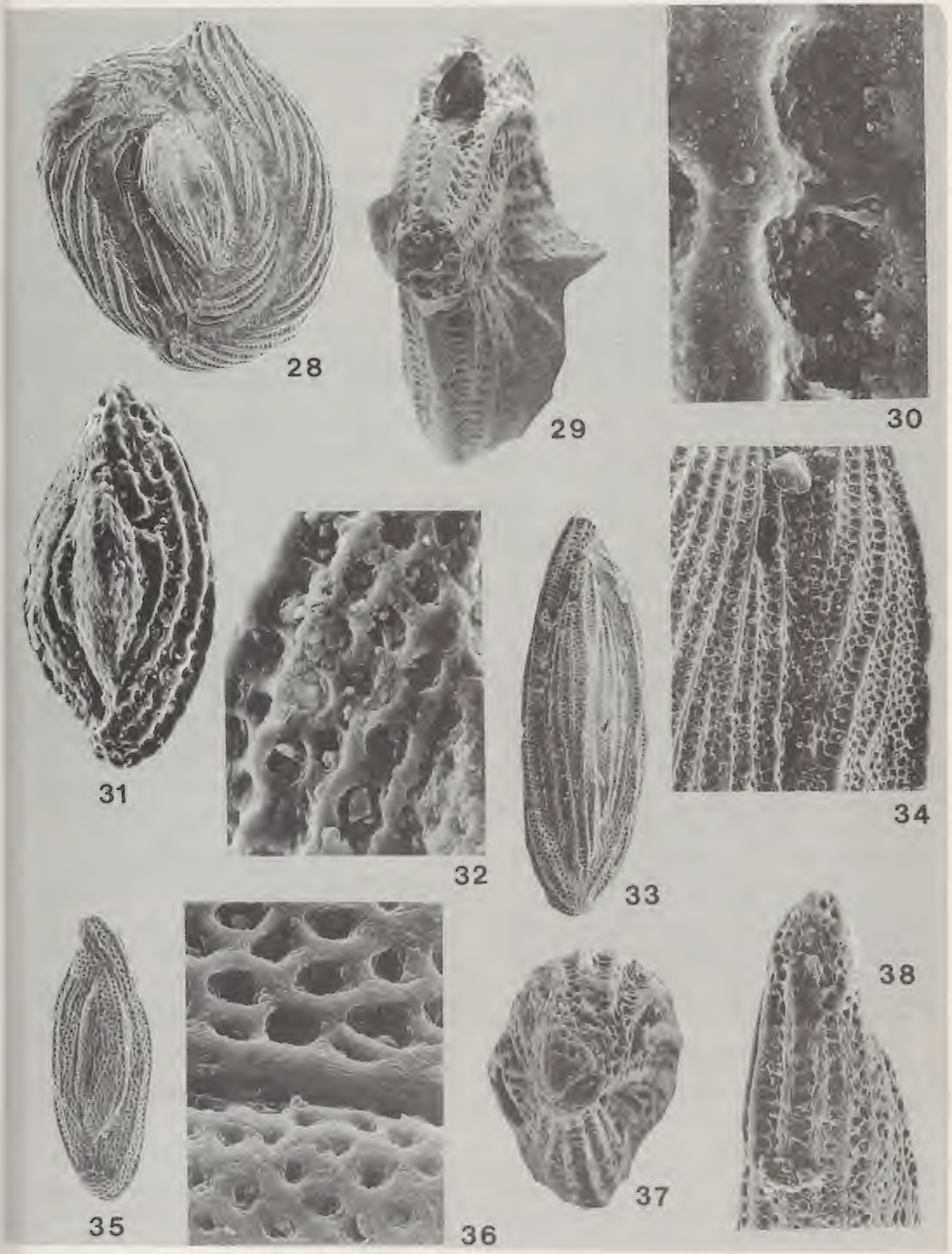
Figures 28-38

Subfamily HELENTAPPANELLINAE Andersen, new subfamily
Helentappanella punctatocostata (Cushman)
28. Lateral view X 25
29. Apertural view X 100
30. Enlargement of pits, showing pores at base of pits X 1000

Subfamily MILIOLACOSTATINAE Andersen, new subfamily
Miliolacostata byramensis (Cushman)
31. Lateral view X 150
32. Eyelets in costae X 500
Miliolacostata jacksonensis (Cushman)
33. Lateral view X 33
34. Enlargement of costae and pits X 80
Miliolacostata rolandi (Andersen)
35. Lateral view X 50
36. Enlargement of pits X 1000
Picouina mississippiensis (Cushman)
37. Apertural view X 300
38. Side view of aperture X 200



Figures 28-38

the anomalous dichotomy which has existed within the Superfamily Miliolacea since the first "perforate miliolids" were described.

V. STRATIGRAPHIC OCCURRENCES

With the exclusion of imperforate porcelaneous Foraminiferida from the Miliolidae, the geological range of the family in the marine deposits of the Gulf Coastal Plain is from the lower Claiborne [Eocene] to the Miocene strata. None of the pitted forms have been reported from the Holocene of the Gulf of Mexico. The known distribution of genera and species from representative Gulf Coastal Plain formations is shown in Table II.

Basal Claiborne Group

The Weches Formation in Texas and the Cane River Formation in Louisiana, both from the base of the Claiborne Group, are the oldest lithologic units in the Gulf Coastal Plain known to contain genera from the Family Miliolidae. *Texina ferayi* Andersen is one of the miliolid species present in the Weches Formation and *Heteromiliola decorata* (Cushman) is the only miliolid species reported from the Cane River Formation (see Table II).

Basal Jackson Group

The Moodys Branch Formation, at the base of the Jackson Group [Eocene Series], is the next youngest lithologic unit bearing miliolids and, in Mississippi, contains major concentrations of miliolid species, including forms from the genera *Miliola, Helentappanella, Hemimiliola,* and *Miliolacostata.* Peculiarly, however, there are none in Moodys Branch outcrops in Louisiana.

Upper Jackson and Ocala Groups

The Upper Eocene Series consists of formations in the Jackson and Ocala groups. The lithologic units studied for this report are the Shubuta and Yazoo formations from the Jackson Group in Mississippi and Alabama, and the Crystal River Formation in Florida. The miliolids recovered from these formations are from the genera *Miliola* and *Heteromiliola.*

Oligocene Series

Three major marine formations within the Oligocene strata were examined for the miliolids present: the Rosefield Formation in Louisiana and the Red Bluff and Byram formations in Mississippi. The highest concentration of miliolids in the Oligocene beds is from the Glendon-Byram outcrop on the right bank of the Pearl River at Byram, Mississippi. Genera present include: *Miliola, Neaguites, Heteromiliola, Miliolacostata,* and *Picouina.*

Miocene Series

The Chipola Formation in Florida is the youngest formation in the Gulf Coastal Plain known to contain a miliolid species. The single species present, *Miliola chipolensis,* is not only the youngest but also the most striking and different.

VI. ENVIRONMENTAL IMPLICATIONS

The upper marine Lutetian outcrops in France are the type area for the Miliolidae and the beds from which the genotype species, *Miliola saxorum*, was described by Lamarck in 1804. Samples collected at the park of the National School of Agriculture at Grignon, France, are from a friable, sandy limestone renowned for the numbers of species present and the preservation of these microfossils. Not only are the true Miliolidae well represented but also the porcelaneous genera previously included within the miliolids.

In the Gulf Coastal Plain, the unit equivalent to the Grignon Lutetian beds, though not quite as sandy, is the Ocala Group in Florida within which *Miliola* is the dominant miliolid genus. It appears that the preferred environment where miliolids flourished, thus, is a relatively warm and shallow [inner neritic], extremely calcareous, near reefal environment.

West of Florida, along the strike of the Jackson Group outcrops, the sediments in Alabama and Mississippi become less calcareous with essentially only marly clay deposits present in Louisiana. It is evident that, at the time of deposition of the Moodys Branch Formation in Mississippi, the waters were not sufficiently calcareous to accommodate the presence of *Neaguites, Heteromiliola, Miliolacostata*, and

TABLE II

Miliolidae Genera and Species in the Gulf Coastal Plain

GENERA AND SPECIES	EOCENE					OLIGOCENE			MIOCENE
	Weches Fm.	Cane River Fm.	Moodys Branch Fm.	Yazoo Fm.	Crystal River Fm.	Rosefield Fm.	Red Bluff Fm.	Byram Fm.	Chipola Fm.
Miliola alphillipsi								●	
" chipolensis								?	●
" newberryensis					●				
" saxorum			●	●					
Hemimiliola jacksonensis			●						
Neaguites byramensis								●	
" inusitatus							●		
Heteromiliola decorata		●		●		●	●	●	
Texina ferayi	●								
Helentappanella punctatocostata			●						
Miliolides byramensis								●	
" jacksonensis			●						
" rolandi								●	
Picouina mississippiensis								●	

Picouina. These four genera, based upon their association with pelagic genera, are adapted to life in the middle to outer neritic zones. It is curious that the Moodys Branch Formation in Louisiana lacks miliolid species though the lithologies of the Moodys Branch Formation in Louisiana and Mississippi are essentially the same.

VII. ACKNOWLEDGMENTS

I wish to thank the following for their contributions: Dr. Joseph Hazel and Dr. Gary Byerly, Chairmen of the Louisiana State University Geoscience Department, for providing the use of a scanning electron microscope; Kasana Pipakpaivan and Emil Platon, LSU graduate students, for operating the SEM and processing photomicrographs for this paper; Alvin Phillips, Jr., Curator of the LSU micropa-

leontology collections, for preparing specimens for the SEM; Dr. Ray E. Ferrell, Jr., LSU Geoscience Department, for an X-ray diffraction analysis of *Heteromiliola decorata* tests to ascertain their chemical composition; Edward B. Picou, Jr., micropaleontological consultant, who read and delivered the manuscript to Tulane University; and, Drs. Emily H. Vokes and Hubert C. Skinner, Editors of this journal, for considering this article important enough to be published in their series.

VIII. REFERENCES CITED

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December 30, 1997

PALEONTOLOGY OF THE MISSISSIPPI RIVER MUDLUMPS: A REASSESSMENT OF THEIR FORAMINIFERAL FAUNA

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I. ABSTRACT

The Mississippi River Mudlumps are diapiric submarine prominences or islands, which occur within the mouths [or passes] of the Mississippi River. The foraminiferal assemblage of the Mudlumps was described by this writer in 1961 based upon the prolific faunules of Foraminiferida from these features, especially those located near the end of South Pass. This microfauna as described originally included numerous species with generic placements that are no longer valid. The new generic assignment for each of these taxa is listed herein and two new genera, *Picouella* and *Tidwellella,* are described to accommodate species that cannot be placed in existing genera.

II. INTRODUCTION

In 1961, a description of the foraminiferal assemblage of the Mississippi River Mudlumps was published as Geological Bulletin No. 35 of the Louisiana Geological Survey. These Mudlumps are diapiric submarine prominences or islands, which occur within the mouths [or passes] of the Mississippi River. The generic placements, as recognized at this early date, for many species are no longer valid. The corrected generic assignments for these species, as now recognized, are presented in Table I below. Two new genera are proposed and described herein for two species that cannot now be placed in existing available genera.

The taxonomic assignments of several decades ago were based on the best information available as viewed through the binocular microscope. Study with the Scanning Electron Microscope [an innovation developed about the time this study was completed] in subsequent years resulted in extensive modification of the classification of the Order Foraminiferida, utilizing elements of the wall structure and other features not visible with clarity under the binocular microscope. The fauna of the Mudlumps included twenty-seven species that must be reassigned, two species for which the species group names must be changed, and two species that cannot be placed in existing valid genera. These taxonomic changes are presented herein as Table I. The descriptions of the two new genera, *Picouella* and *Tidwellella*, follow below.

III. SYSTEMATIC DESCRIPTIONS

Genus PICOUELLA, new genus

Type species: *Cibicides corpulentus* Phleger and Parker, 1952.

Diagnosis: Test free, trochospiral, biconvex, eleven to thirteen chambers per volution, sutures limbate and elevated, periphery rounded; wall calcareous with granular microstructure; spiral side with secondary thickening of clear calcite concealing coils preceding final whorl; involute side with thickened, clear boss in umbilicus; both sides of test coarsely perforate; aperture interiomarginal and equatorial with lip. Known occurrence: Pleistocene and Holocene, Gulf of Mexico.

Remarks: This genus differs from *Cibicides* in being biconvex and having most of the early chambers covered by the thick mass of secondary clear calcite and from *Anomalinoides* in the larger number of chambers per volution and in the elevated and limbate sutures that thicken to produce the boss at the center of the involute side of the test.

This genus in named for Edward B. Picou, Jr., in appreciation for his friendship and contributions to my life, and in recognition of his superior knowledge in the geology and paleontology of the Gulf Coastal Plain region.

Taxonomic Note: Professor Barum K. Sen Gupta of the Geology and Geophysics Department, Louisiana State University, has directed my attention to an article in

the *Journal of Foraminiferal Research* (vol. 24, no. 4, pp. 296-304, October 1994). This article, by Stephen A. Revets, Department of Geology and Geophysics, University of Western Australia, is titled "The Status of the Genus *Anomalina* d'Orbigny, 1826," and includes an appeal to the International Commission on Zoological Nomenclature ".... to set aside *A. punctulata* as type species [of *Anomalina*] and instate *A. ariminensis* as the type species." If the ICZN, utilizing its plenary powers, accepts this proposal, the genus *Picouella*, described herein as new, will become a junior synonym of *Anomalina* d'Orbigny, 1826.

PICOUELLA CORPULENTUS
(Phleger and Parker)
Text-figure 1

Truncatulina akneriana FLINT (not d'Orbigny), 1899, U. S. Natl. Mus., Ann. Rept. for 1897, p. 333, pl. 77, fig. 5.

Cibicides robustus PHLEGER and PARKER, 1951, Geol. Soc. America, Mem. 46, pt. 2, p. 31, pl. 17, figs. 1-4; not *Cibicides robustus* Le Calvez, 1949, Mém. Explic. Carte Géol. dét. France, p. 47, pl. 4, figs. 57-59. [Lutetian, Paris Basin, France]

Cibicides corpulentus PHLEGER and PARKER, 1952, Cushman Found. Foram. Res., Contr., vol. 3, pt. 1, p. 14.

"Cibicides" corpulentus Phleger and Parker. ANDERSEN, 1961, Louisiana Geol. Surv., Geol. Bull. 35, pt. 2, p. 123, pl. 2, figs. 1a-c.

Diagnosis: Test low, trochospiral, nearly biconvex, eleven to thirteen chambers per volution, increasing in size as added and tapering to a rounded periphery bearing a band of clear, perforate calcite on its perimeter; chambers coarsely perforate on both sides of test; on spiral side chambers of final whorl nearly concealing the previous ones; chambers separated by limbate, elevated sutures that thicken and coalesce on proximal (inner) portion of chambers, producing a channel between coils extending into secondary thickening at center of spiral side; sutures radiating from clear boss at umbilicus, with only a slight curve at their distal ends near periphery; aperture interiomarginal and equatorial, extending to base of final one or two chambers on spiral side of test; with a small imperforate lip on equatorial portion of final chamber.

Remarks: As early as 1961, it was evident that *Cibicides* was incorrect as placement for this species. In 1988, this was confirmed by the restriction of *Cibicides* by Loeblich and Tappan to include only those species that are "planoconvex, [with] spiral side flat to concave" and with "test commonly attached to a substrate." However, no genus with generic characteristics of *Picouella corpulentus* was described by these authors. This species is abundant in Mudlump SP-5 and is widespread in the Gulf Coast region and fully worthy of recognition as a new and separate genus.

Genus TIDWELLELLA, new genus

Type species: *Planulina exorna* Phleger and Parker, 1951.

Diagnosis: Test free, trochospiral, strongly flattened or compressed, eight to ten chambers per volution; wall calcareous with granular microstructure; spiral side flat, may have secondary lamellae at center of coil; umbilical side partially or fully evolute; aperture interiomarginal with imperforate lip. Known occurrence: Pleistocene and Holocene, Gulf of Mexico.

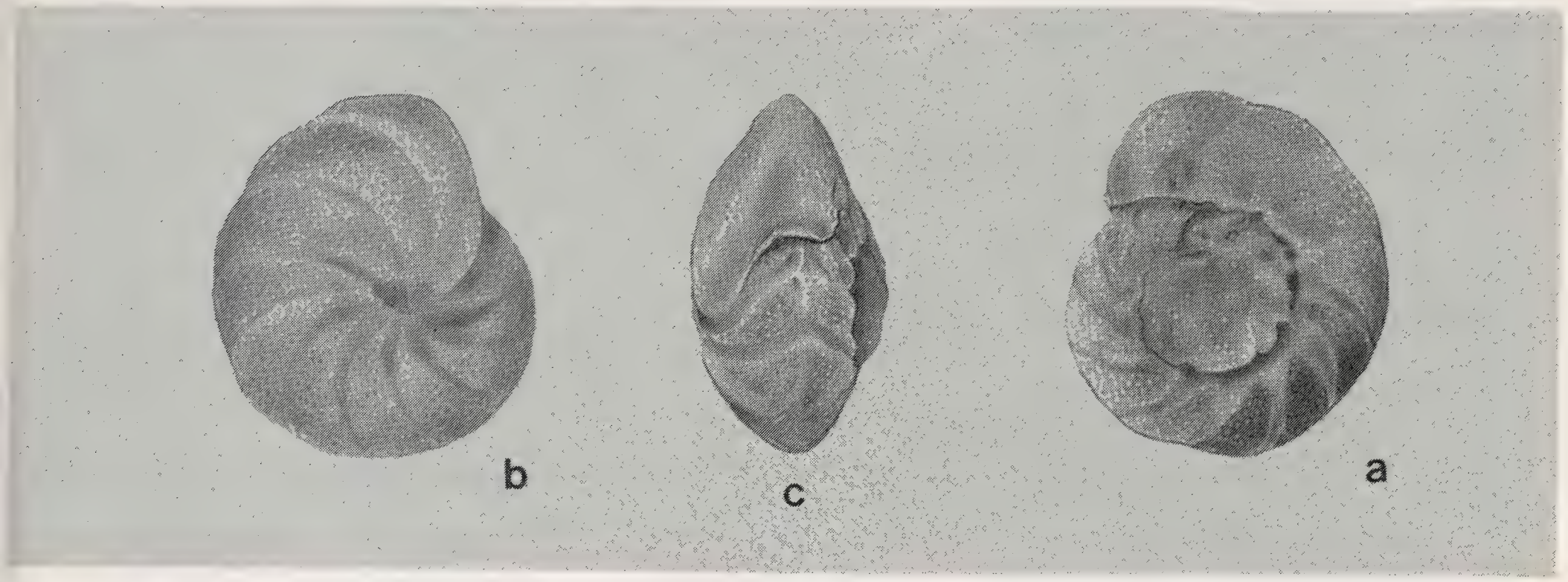
Remarks: This genus accomodates those flattened, trochospiral foraminiferal genera that are partially to entirely evolute but lacking the truncated perimeter of the genus *Planulina*. This genus is named for William L. Tidwell in appreciation for the sentiments expressed in his acknowledgments in the "Comprehensive Index of the GCAGS Transactions," published in May 1984, and for his contributions to his alma mater, Louisiana State University.

TIDWELLELLA EXORNA (Phleger and Parker)
Text-figure 2

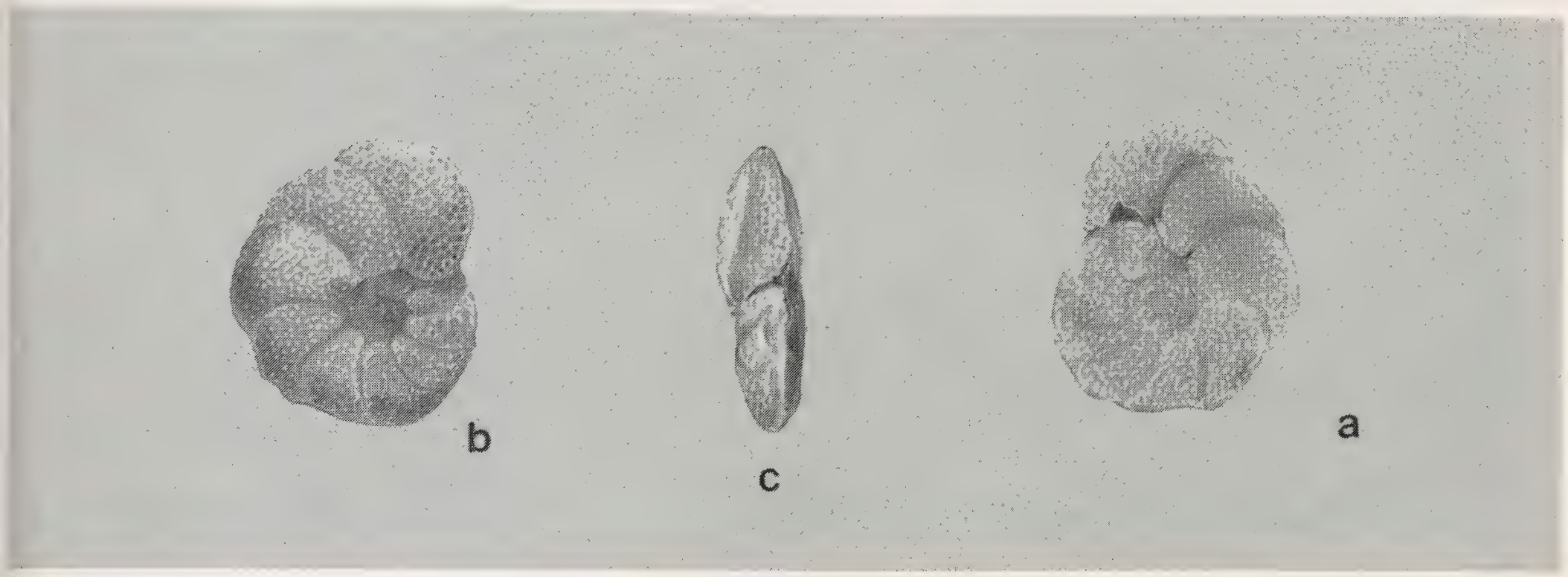
Planulina exorna PHLEGER and PARKER, 1951, Geol. Soc. America, Mem. 46, pt. 2, p. 32, pl. 18, figs. 5-8; PARKER, 1954, Museum Comp. Zool., Bull., vol. 111, no. 10, p. 504, pl. 11, figs. 28, 29.

Planulina mera Cushman. ANDERSEN, 1961, Louisiana Geol. Surv., Geol. Bull. 35, pt. 2, p. 125, pl. 29, figs. 3a-c.

Diagnosis: Test flattened, thin, eight to ten chambers per volution; wall coarsely perforate, including face of last formed chamber; sutures curved and limbate; spiral side flat to slightly



Text-figure l. *Picouella corpulentus* (Phleger and Parker). X 40
No. 4480* a. spiral view; b. umbilical view; c. edge view.



Text-figure 2. *Tidwellella exorna* (Plhleger and Parker). X 40
No. 4478* a. spiral view; b. umbilical view; c. edge view.

depressed with secondary filling at center concealing primary coil; final two or three chambers lobate with depressed sutures; umbilical side equally as evolute as spiral side; chambers increasing in breadth with maximum thickness of last chamber nearly aligned with aperture, tapering from that point to periphery; aperture interiomarginal, equatorial, confined to last chamber of test, with a small, imperforate lip.

Remarks: The warped nature of some specimens indicates that at least some individuals were attached to the substrate like *Cibicides.*

• Numbers refer to the Dr. H. V. Howe Paleontological Collection, LSU.

IV. ACKNOWLEDGMENTS

The writer wishes to express his gratitude to the following for their contributions to this report: Dr. Gary Byerly, Chairman of the Geoscience Department, Louisiana State University (LSU), for the use of a petrographic microscope to ascertain the microstructure of the new foraminiferal genera described herein; Alvin Phillips, Jr., Curator of the Micropaleontological Collections, LSU, for assistance with the petrographic microscope; William Marsalis, State Geologist of Louisiana, for permission to use illustrations of the holotypes of the two new genera described herein, first published

[1961] in Louisiana Geological Survey Geological Bulletin No. 35; and, Drs. Emily H. Vokes and Hubert C. Skinner, Editors of *Tulane Studies in Geology and Paleontology,* for evaluating this report.

V. REFERENCES CITED

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December 30, 1997

TABLE I. Taxonomic Changes for Species Cited in Andersen, 1961

OLD NAME [1961]	PLATE: FIGURE(s)	REVISED NAME [1997]
Lenticulina peregrina (Schwager)	Pl. 10: 7a, b	*Neolenticulina peregrina* (Schwager), 1866
Robulus lowmani Andersen	Pl. 10: 8a, b	*Lenticulina lowmani* (Andersen), 1961
Robulus sp. "H"	Pl. 10: 9a, b	*Lenticulina* sp. "H"
"Robulus" cf. *R. serpens* (Seguenza)	Pl. 10: 10a, b	*Lenticulina* cf. *L. serpens* (Seguenza), 1880
Robulus calcar (Linnaeus)	Pl. 11: 1a, b; 2a, b	*Lenticulina calcar* (Linnaeus), 1767
Robulus sp. "B"	Pl. 11: 3a, b	*Lenticulina* sp. "B"
Robulus sp. "F"	Pl. 11: 4a, b	*Lenticulina* sp. "F"
Robulus sp. "G"	Pl. 11: 5a, b	*Lenticulina* sp. "G"
Robulus sp. "D"	Pl. 12: 1a, b	*Lenticulina* sp. "D"
Robulus sp. "C"	Pl. 12: 2a, b	*Lenticulina* sp. "C"
Robulus sp. "A"	Pl. 12: 3a, b	*Lenticulina* sp. "A"
Robulus bowdenensis (Cushman)	Pl. 12: 4a, b	*Lenticulina bowdenensis* (Cushman), 1919
Robulus sp. "E"	Pl. 13: 1a, b	*Lenticulina* sp. "E"
Robulus cf. *R. cultratus* Montfort	Pl. 13: 2a, b	*Lenticulina* cf. *L. cultratus* (Montfort), 1808
Robulus cf. *R. falcifer* (Stache)	Pl. 13: 3a, b	*Lenticulina* cf. *L. falcifer* (Stache), 1864
Robulus iotus (Cushman)	Pl. 13: 4a, b	*Lenticulina iotus* (Cushman), 1923
Marginulina villa Cushman	Pl. 14: 6a, b; 7a, b	*Siphomarginulina villa* (Cushman), 1947
Marginulina obesa Cushman	Pl. 15: 2a, b	[?] *Hemirobulina obesa* (Cushman), 1923
Marginulina cf. *M. glabra* d'Orbigny	Pl. 15: 6a, b	[?] *Hemirobulina* cf. *H. glabra* (d'Orbigny), 1826
Marginulina striatula Cushman	Pl. 15: 7a, b; 8a, b	[?] *Hemirobulina striatula* (Cushman), 1923
Marginulinopsis marginulinoides (Goës)	Pl. 15: 9a, b	*Percultazonaria marginulinoides* (Goës), 1896
Marginulinopsis subaculeata glabrata (Cushman)	Pl. 15: 10a, b	*Percultazonaria subaculeata glabrata* (Cushman), 1923
Vaginulinopsis planata (Phleger & Parker)	Pl. 15: 11	*Percultazonaria planata* (Phleger & Parker), 1951
Vaginulinopsis sp.	Pl. 15: 12a, b; 13	*Percultazonaria* sp.
"Nodosaria" pyrula d'Orbigny	Pl. 16: 1	*Grigelis guttifera* (d'Orbigny), 1826

Amphorina purii Andersen	Pl. 16: 6	*Lagena purii* (Andersen), 1961
Lagena halsteadi Andersen	Pl. 16: 10	*Pytina halsteadi* (Andersen), 1961
Lagena spirata Bandy	Pl. 16: 12	*Lagena striata* (d'Orbigny), 1839
Lagena inusitata Andersen	Pl. 16: 14	*Pytina inusitata* (Andersen), 1961
Lagena striata (d'Orbigny)	Pl. 16: 15	*Lagena spirata* Bandy, 1949
Dentalina sp.	Pl. 17: 2	*Marginulina* sp.
Dentalina cf. *D. subemaciata* Parr	Pl. 17: 3	*Laevidentalina* cf. *L. subemaciata* (Parr), 1950
Dentalina filiformis (d'Orbigny)	Pl. 17: 4	*Laevidentalina filiformis* (d'Orbigny), 1829
Pseudonodosaria comatula (Cushman)	Pl. 17: 9	[?] *Pyramidulina comatula* (Cushman), 1923
Nodosaria albatrossi Cushman	Pl. 17: 11	*Dentalina cuvieri* (d'Orbigny), 1826
Nodosaria fusta Cushman and Todd	Pl. 17: 12	[?] *Pyramidulina fusta* (Cushman and Todd), 1945
Pseudononion grateloupi (d'Orbigny)	Pl. 18: 3	*Nonionides grateloupi* (d'Orbigny), 1826
"Nonion" barleeanus (Williamson)	Pl. 18: 6	*Melonis barleeanus* (Williamson), 1858
Elphidium fimbriatulum (Cushman)	Pl. 18: 9	*Cribroelphidium fimbriatulum* (Cushman), 1918
Elphidium cf. *E. translucens* Natland	Pl. 18: 10	*Cribroelphidium* cf. *C. translucens* (Natland), 1938
Praesorites orbitolitoides Hofker	Pl. 19: 1	New undescribed genus
Loxostomum gelbi (Andersen)	Pl. 19: 7	[?] *Sagrina gelbi* (Andersen), 1961
Virgulina punctata d'Orbigny	Pl. 20: 1	*Fursenkoina punctata* (d'Orbigny), 1839
Virgulina complanata Egger	Pl. 20: 2	*Fursenkoina complanata* (Egger), 1893
Virgulina pontoni (Cushman)	Pl. 20: 3	*Fursenkoina pontoni* (Cushman), 1932
Bolivina cf. *B. albatrossi* Cushman	Pl. 20: 5	*"Bolivina"* cf. *B. albatrossi* Cushman, 1922
Bolivina barbata Phleger and Parker	Pl. 20: 6	*Brizalina barbata* (Phleger and Parker), 1951
Bolivina mexicana Cushman	Pl. 20: 7	*Brizalina mexicana* (Cushman), 1922
Bolivina fragilis Phleger and Parker	Pl. 20: 8	*Brizalina fragilis* (Phleger and Parker), 1951
Bolivina spinata Cushman	Pl. 20: 11	*Bolivinellina spinata* (Cushman), 1936
Discopulvinulina bertheloti (d'Orbigny)	Pl. 21: 3	*Discorbinella bertheloti* (d'Orbigny), 1939
Streblus beccarii tepida (Cushman)	Pl. 22: 2	*Strebolides beccarii tepida* (Cushman), 1926
Neoeponides regularis (Phleger and Parker)	Pl. 23: 3	*Eponides regularis* Phleger and Parker, 1951
Neoeponides antillarum (d'Orbigny)	Pl. 23: 4, 5	*Eponides antillarum* (d'Orbigny), 1839
"Eponides" cf. *E. tumidulus* (H.B. Brady)	Pl. 24: 5	[?] gen. et sp. undet.

Cassidulina subglobosa H.B. Brady	Pl. 25: 2	*Globocassidulina subglobosa* (H.B. Brady), 1884
Cassidulinoides mexicana (Cushman)	Pl. 25: 5	*Rutherfordoides mexicana* (Cushman), 1922
Globorotalia (Turborotalia) sp.	Pl. 26: 1	*Turborotalia* sp.
Globorotalia (Truncorotalia) cf. *Globorotalia hirsuta* (d'Orbigny)	Pl. 26: 2	*Truncorotalia* cf. *T. hirsuta* (d'Orbigny), 1839
Globorotalia (Truncorotalia) truncatulinoides (d'Orbigny)	Pl. 26: 3	*Truncorotalia truncatulinoides* (d'Orbigny), 1839
Globigerina eggeri Rhumbler	Pl. 27: 2	*Neogloboquadrina dutertrei* (d'Orbigny), 1839
Globigerinoides conglobatus (H.B. Brady)	Pl. 27: 5	*Alloglobigerinoides conglobatus* (H.B. Brady), 1879
Epistomina elegans (d'Orbigny)	Pl. 28: 4	*Hoeglundina elegans* (d'Orbigny), 1826
Cibicides floridanus (Cushman)	Pl. 28: 6	*Cibicidoides floridanus* (Cushman), 1918
"Cibicides" corpulentus Phleger and Parker	Pl. 29: 1	*Picouella corpulentus* (Phleger and Parker), 1952 [new genus]
Anomalina io (Cushman)	Pl. 29: 2	[?] *Anomalinoides io* (Cushman), 1931
Planulina mera Cushman	Pl. 29: 3	*Tidwellella exorna* (Cushman), 1944 [new genus]

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A NEW SPECIES OF *PTERYNOTUS* (GASTROPODA: MURICIDAE) FROM THE EOCENE OCALA LIMESTONE OF FLORIDA

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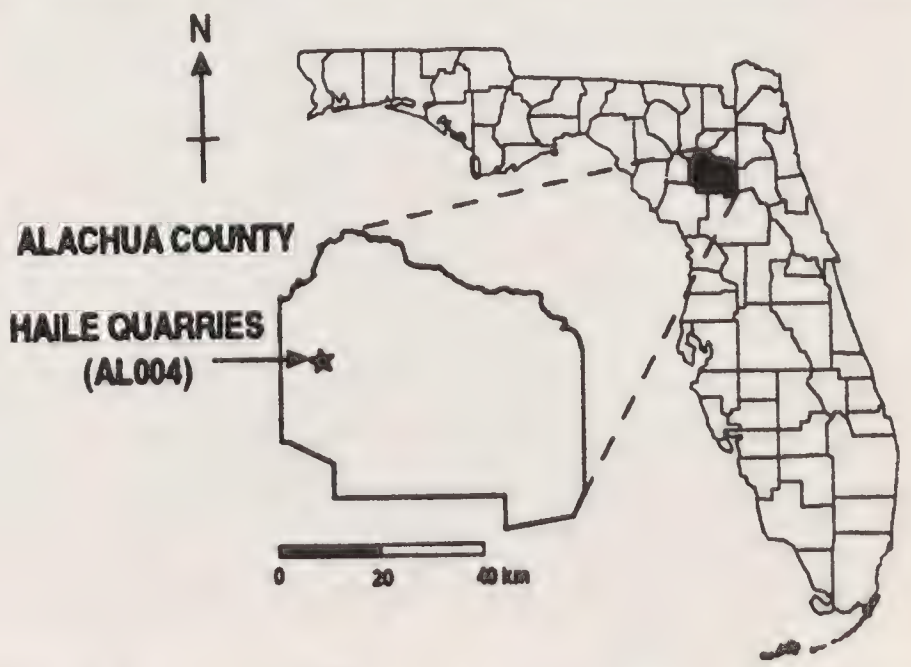
A new species of gastropod belonging to the genus *Pterynotus* is described herein from the middle to late Eocene Ocala Limestone of Florida. Vokes (1970, p.11) first reported the occurrence of *Pterynotus* from the Ocala Limestone based upon a single specimen, discovered in 1961 by R. D. Suttkus, from a quarry complex near the town of Newberry, Alachua County, Florida (Tulane University locality TU 449). Awaiting additional material, Vokes (1970) made a preliminary identification of the specimen. Intensive collecting at the University of Florida (UF) locality AL004 (see Text-figure 1) by the senior author and staff and volunteers of the Invertebrate Paleontology Division of the Florida Museum of Natural History (FLMNH), during the last ten years has yielded two additional Ocala Limestone *Pterynotus*. Together, these three exceedingly rare Eocene specimens provide the data upon which our new species is based. All three (UF 68400, UF 71286, and UF 71287) are reposited in the Type Collection at the FLMNH. At UF locality AL004 most limestone is dredged underwater and brought to the surface. Therefore, the exact stratigraphic placement of the above mentioned specimens within the lower, middle, or upper Ocala Limestone is not possible.

The middle to late Eocene Ocala Limestone (equals the Ocala Group) is exposed at the surface in northwestern peninsular Florida and a small portion of the Florida panhandle (along the border with Georgia and Alabama). The unit contains a diverse invertebrate fauna, especially molluscs, which have yet to be thoroughly studied. The lack of critical review of the molluscan fauna is primarily due to poor preservation. The aragonitic molluscs normally occur as casts and molds and the calcitic molluscs are typically thin and fragile. However, new techniques for collecting specimens and new laboratory techniques (*e.g.*, producing silicone rubber peels of the external molds) have greatly enhanced our ability to identify many of these previously unknown and currently undescribed taxa. The silicone peel technique was used to facilitate the description of the new *Pterynotus* species below. For a detailed discussion on the stratigraphic nomenclature of the Ocala Limestone (Ocala Group) see Oyen (1995) and Jones (1997).

ACKNOWLEDGMENTS

Greta and Andrew Murray, Bradenton, Florida, are thanked for collecting and donating the holotype specimen (UF 71286). Russ McCarty and Craig Oyen, Florida Museum of Natural History, provided assistance with the making of silicone peels and photography, respectively. Laurie Walz, University of Florida, kindly drafted Text-figure 1. This and additional studies (in progress), by the senior author and others, on the Florida Eocene macroinvertebrates have been facilitated by the transfer of materials from the Paleontological Research Institution (PRI), Tulane University Geology Department (TU), Florida State University Geology Department, Florida Geological Survey, and the Muriel Hunter Collection to the FLMNH. David Nicol, generously con-



Text-figure 1. Florida map showing collecting location of *Pterynotus rogersi,* n. sp. (UF locality AL004).

tributed $1,000 to help defray the cost of packing and shipping the Florida Eocene mollusc collection of the late Katherine Palmer from the PRI to the FLMNH. Although not used in this study, David Campbell, University of North Carolina, Chapel Hill is thanked for sharing information about specimens of Eocene *Pterynotus* that he collected in South Carolina and North Carolina. This is University of Florida Contribution to Paleontology 495.

SYSTEMATIC PALEONTOLOGY

Class GASTROPODA
Order NEOGASTROPODA
Superfamily MURICACEA
Family MURICIDAE Rafinesque, 1815
Genus PTERYNOTUS Swainson, 1833

Pterynotus SWAINSON, 1833, Zool. Illus., (Ser. 2) v. 3, expl. to pl. 100.

Type species: *Murex pinnatus* Swainson, 1822, by subsequent designation, Swainson, *ibid.*, pl. 122.

PTERYNOTUS (PTERYNOTUS) ROGERSI
Portell and Vokes, n. sp.
Plate 1, figures 1-3

Description: Earliest whorls not preserved but at least six teleoconch whorls, each ornamented by three winged varices, with one low axial node between each pair of varices; intervarical areas smooth except for spiral cords. Varices flaring, crenulated by spiral ornamentation; each varix joined to corresponding varix of previous whorl, forming a continuous, slightly curved line up spire. Abapertural varical faces festooned with multiple laminae, elaborately scalloped in harmony with spiral cords. Spiral ornamentation on earliest preserved whorls of two cords; one at shoulder, a second weaker one between shoulder and suture, and a third weakest cord sometimes on subsutural ramp. About six spiral cords on body whorl, with an additional two cords on siphonal canal. Suture appressed, subsutural ramp concave inward. Aperture elongate-oval, inner lip smooth appressed at posterior end, probably free-standing at anterior end. Inner side of outer lip with about six strong denticles, corresponding to spaces between spiral cords. Margin of outer lip projecting in advance of varix, also scalloped by spiral cords, especially at shoulder with a small infolding onto shoulder spiral. Siphonal canal broad, open by a narrow slit; a lamellar extension of each varix along entire length; slightly recurved at distal end.

Holotype: UF 71286; partial external mold of dorsal side, maximum length of incomplete external mold 38.0 mm, maximum width of incomplete external mold 21.2 mm (Plate 1, fig. 1a).

Type locality: UF locality AL004, Dickerson Limerock Mines (Haile Complex), approximately 5.0 miles northeast of Newberry along State Road 235, near the now defunct town of Haile, Alachua County, Florida (Sec. 13, 23-26, T9S, R17E; Newberry Quadrangle, USGS 7.5' series, 1988).

Paratype A: UF 71287; maximum length of incomplete external mold 42.0 mm, width 21.9 mm.

Paratype B: UF 68400; maximum length of incomplete external mold 43.6 mm, width 23.0 mm.

Occurrence: Ocala Limestone, northwestern part of peninsular Florida; middle-late Eocene.

Etymology: Named for Mr. Larry Rogers, Limestone Products, Incorporated, Newberry, Florida, who for many years has allowed staff and volunteers of the FLMNH access to the quarries in the Newberry area, and on many occasions has given the FLMNH assistance with excavations of fossils in the quarries under his supervision.

Discussion: As was noted in Vokes

PLATE 1

Figures

1-3. *Pterynotus rogersi* Portell and Vokes, new species. Locality: UF locality AL004.

1A. UF 71286 (holotype); partial external mold of dorsal side, maximum length of incomplete external mold 38.0 mm, maximum width of incomplete external mold 21.2 mm.

1B. UF 71286 (silicone peel of holotype); maximum length 38.0 mm, maximum width 21.2 mm.

2. UF 68400 (silicone peel of paratype B); maximum length 43.6 mm, maximum width 23.0 mm.

3. UF 71287 (silicone peel of paratype A); maximum length 42.0 mm, maximum width 21.9 mm.

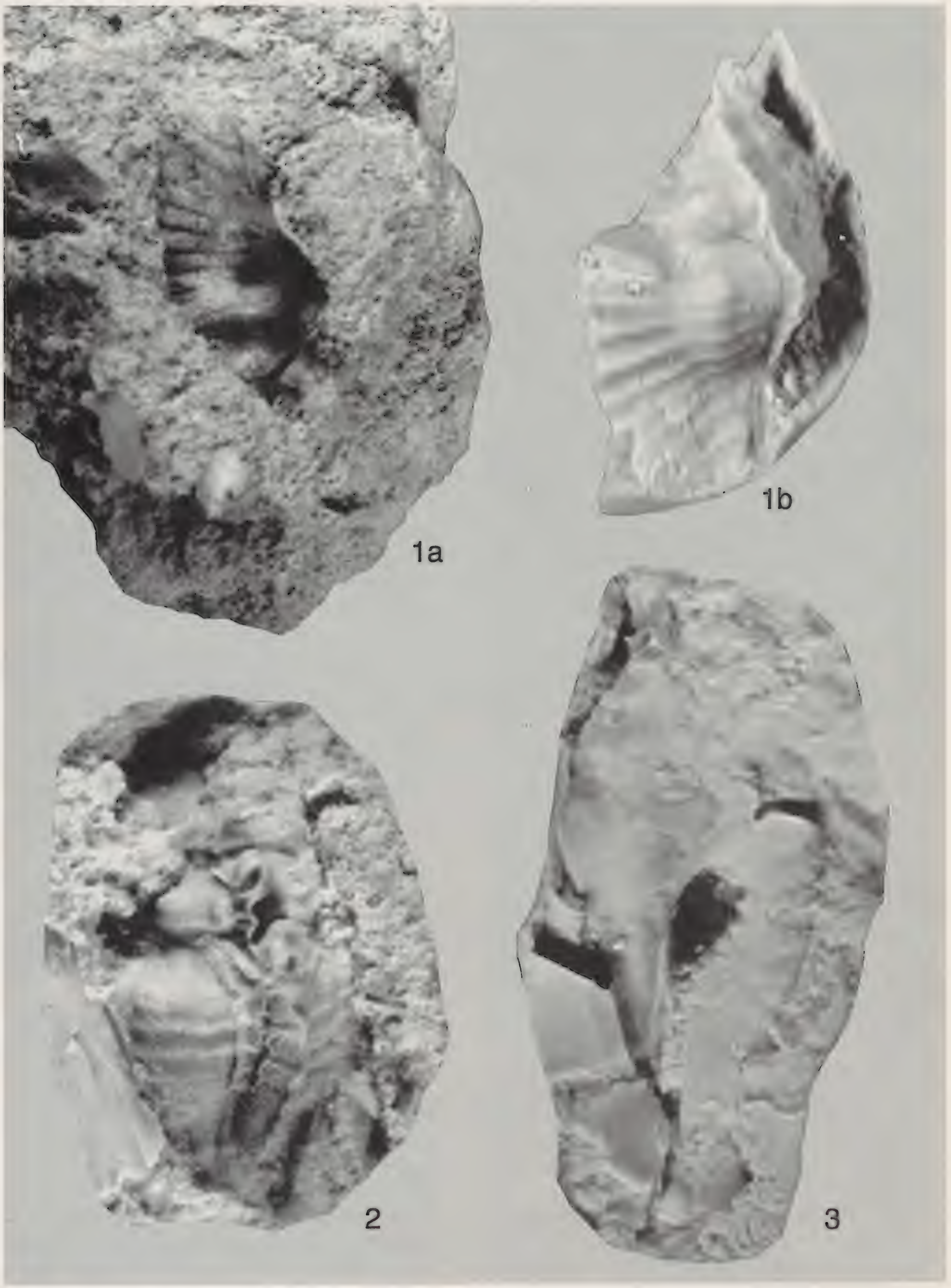


PLATE 1

(1992, p. 4), the species of *Pterynotus* may be divided into five "Species-Groups," with the members of each group having a strong resemblance to each other but having slightly different characteristics from the others. One of the groups, termed therein "Species group 5," (that of *Pterynotus phyllopterus*), consists of several American species ranging in age from early Oligocene to the Recent. In addition, there are species from the Miocene of Italy, as well as the Recent of Australia. All of these species are remarkably alike and all have been presumed to be derived somehow from *P. tripteroides* (Lamarck, 1822), from the Middle Eocene of the Paris Basin.

However, discovery of a new member of this Species Group from the middle to late Eocene Ocala Limestone of Florida causes a re-evaluation of this relationship. All members of the group of *P. phyllopterus* are remarkably alike, differing primarily in the number and relative strength of spiral cords seen in the various species. However, all of the species (including *P. bednalli* Brazier, 1878) differ in one very important character from the French *P. tripteroides*. This distinction is the presence in the latter of a sinuous fold of shell material at the posterior end of the apertural lip, which extends onto the previous whorl and creates a small anal channel in the manner of the oldest species of *Pterynotus* [such as *P. matthewsensis* (Aldrich, 1886), from the Paleocene of Alabama, and *P. stenzeli* Vokes, 1970, from the early Eocene of Texas], thereby suggesting that this is a primitive feature. All of the other members of the group of *P. phyllopterus* have the posterior end of the aperture broadly rounded.

This new species differs from the younger species in the following ways:

(1.) *P. burnsii* (Aldrich, 1894), from the early Oligocene Red Bluff Formation,Mississippi, has more numerous (about 13) spiral cords, including about three relatively strong cords on the subsutural ramp;

(2.) *P. postii* (Dall, 1896), from the late Oligocene Tampa Limestone, Florida, has more numerous (about 15) spiral cords, which are much weaker in the intervarical areas;

(3.) *P. hoerlei* Vokes, 1970, from the early Miocene Chipola Formation, Florida, has about the same number of spiral cords (seven, plus two very weak cords on subsutural ramp), which are essentially absent in the intervarical areas, and which are much broader, causing the varical margins to be more strongly undulating;

(4.) *P. phyllopterus* (Lamarck, 1822) (including probable synonyms *P. perlongus* and *P. rovasendae*, both of Bellardi, 1872, from the Miocene of Italy) has about the same number of spiral cords (nine), which like *P. hoerlei* are poorly developed in the intervarical areas, but which even more strongly undulate the varices; in addition, there are two intervarical nodes in this species, unlike all of the earlier forms.

(5.) *P. bednalli* (Brazier, 1878), from the Recent off northwestern Australia, has about 16 spiral cords and two to three weak intervarical nodes.

LOCALITY DATA

The following is a collecting locality of the Invertebrate Paleontology Division, Florida Museum of Natural History (FLMNH), University of Florida (UF). Tulane University locality TU 449 is equivalent to this locality:

AL004 Dickerson Limerock Mines (Haile Complex), approximately 5.0 miles northeast of Newberry along State Road 235, near the now defunct town of Haile, Alachua County, Florida (Sec. 13, 23-26, T9S, R17E; Newberry Quadrangle, USGS 7.5' series, 1988).

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NOTES ON THE FAUNA OF THE CHIPOLA FORMATION– XLII
A NEW SPECIES OF *OLIVA (OMOGYMNA)* (GASTROPODA: OLIVIDAE)

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The Olivinae of the Alum Bluff Group have been previously reviewed (Drez, 1981) with the description of two new species and one subspecies and the reassignment of previously described species to one new genus and subgenus. Recently during a visit to Tulane University to examine their paleontological collections, a new large species of Olivinae from the Chipola Formation was found in the collections, unlike anything else in the western Atlantic Tertiary. Further examination of the Tulane collections failed to produce an additional specimen.

Family OLIVIDAE Latrielle, 1825
Subfamily OLIVINAE Swainson, 1840
Genus OLIVA Bruguiére, 1789

Oliva BRUGUIÉRE, 1789, Encycl. Méth.(Vers), v. 1, p. XV (genus without named species).

Type species: *Voluta oliva* Linnaeus, 1758 (*Oliva ispidula* of most authors, not of Linnaeus) by tautonomy and monotypy.

Discussion: The reader is referred to Drez (1981) for an explanation of some of the confusion over the assignment of a type species for the genus *Oliva.*

Subgenus OMOGYMNA
von Martens, 1897

Omogymna VON MARTENS, 1897, Conchologische Miscellen II, p. 157.

Type species: *Oliva paxillus* Reeve, 1850, by monotypy.

Discussion: Omogymna is characterized by a depressed posterior band on the body whorl, which may or may not be visible on the spire whorls, depending upon the amount of intrasutural callus. The width of the band may vary considerably from species to species, usually attaining a constant width by maturity. On juvenile specimens the posterior band can occupy up to two-thirds of the body whorl, gradually narrowing and becoming more depressed with maturity. Drez (1981) provided a discussion of the designation of type species for this subgenus.

OLIVA (OMOGYMNA) FARLEYENSIS Drez, n. sp.
Plate 1, figure 1

Description: Shell of large size for the genus, thick and heavy, body whorl smoothly rounded at both ends, slightly inflated, maximum diameter a little posterior to mid-line. Seven to eight whorls in holotype. Defective two+ whorl papillary protoconch. Spire approximately one-sixth of total height, with the profile planar in outline. Transition from protoconch to teleoconch whorl obscure, characterized by a rapid vertical flattening of last nuclear whorl and deepening of suture. The first teleoconch whorl nearly vertical in outline, with tendency to lateral flattening near end of first volution. A ribbon of callus, straight in outline, on early postnuclear whorls bordering posterior edge of previous volution, callus thickening and descending on later whorls and occupying slightly more than half of penultimate whorl with callus just touching anterior edge of posterior depressed band. Suture deeply channeled, narrow, with overhanging ribbon of callus. Depressed posterior band up to 3.0 mm wide with undulating anterior edge. Lip broken at posterior end, but appearing to be narrow, gradually widening anteriorly. Parietal callus heavy at anterior end becoming thinner toward posterior and extending to join callus on penultimate whorl. Approximately eight distinct lirae, stronger anteriorly with some secondary lirae in between, extending up to three-fourths the way to posterior end of columella. One strong and two weaker plications on base of columella, stronger posteriorly, evanescing before reaching siphonal notch. The siphonal fasciolar band intersecting parietal callus on columella a little less than half-way from anterior end of aperture, widening as it cuts obliquely across columella toward siphonal notch, fading around notch. Siphonal notch moderately deep, sides slightly flaring.

Holotype: USNM 496494; height 50.6 mm, maximum diameter 21.6 mm.

Type locality: TU 819, Chipola Formation; Farley Creek, 0.2 mile west of bridge of Florida

Highway 275 (SW 1/4 Sec. 21, T1N, R9W), Calhoun County, Florida.

Etymology of name: for Farley Creek, Calhoun County, Florida, origin of the holotype.

Occurrence: Chipola Formation, Florida.

Figured specimen: USNM 496494 (holotype).

Discussion: It is unfortunate that only one specimen of this impressive species has been found in the Chipola Formation, and that specimen is damaged.

Previously (Drez, 1981), *Oliva liodes* (Dall, 1903) was assigned to the subgenus *Omogymna* based on the occurrence of a minute depressed posterior band on the whorls (1.2 mm or less)(pl. 1, fig. 2). The posterior band on *O. farleyensis* is much thicker (3.0 mm) and is as thick as the posterior band on the body whorl (after reaching a constant width) of the type species of the subgenus *Omogymna, Oliva paxillus* Reeve (pl. 1, fig. 3).

Because of the large size of *O. farleyensis* as a species of the subgenus *Omogymna*, there are only two other species described which might be confused with *O. farleyensis: O. liodes* Dall, 1903, from the Chipola Formation and *O. valens* Jung (1971, pl. 13, figs. 7, 8), from the early middle Miocene of Carriacou, West Indies. *Oliva farleyensis* may be discriminated from contemporaneous *O. liodes* by its larger size, wider posterior band, and more rounded outline. Jung figured the holotype (pl. 13, fig. 7) and paratype (pl. 13, fig. 8) for *O. valens. Oliva farleyensis* can be separated from the holotype of *O. valens* by its larger size, planar outline for the spire, and wider posterior depressed band. The holotype and paratype of *O. valens* differ in outline and may actually be a mixture of two species of *Omogymna.*

The occurrence of two large species of *Omogymna, O. liodes* and *O. farleyensis* in a single formation (Chipola) is unique, since the only other occurrence of a large species of *Omogymna* is from Carriacou. Jung (1971) tentatively assigned *O. valens* to the subgenus *Omogymna* because of its large size, as no comparably sized species of *Omogymna* had been described at that time. The occurrence of the two large species of *Omogymna, O. liodes* and *O. farleyensis,* in the Chipola Formation confirms the tentative assignment of the similar *O. valens* to *Omogymna* by Jung (1971).

In addition to *O. liodes* and *O. farleyensis*, the Chipola also contains another species of *Omogymna, O. martensii* Dall, 1903 (see Drez, 1981). This gives the Chipola Formation the distinction of being the only known formation with three species of *Omogymna.*

ACKNOWLEDGMENTS

The author would like to thank Dr. Emily Vokes for providing the holotype, access to the Tulane University paleontology collections and for reviewing this paper. Dr. Vokes is also responsible for encouraging this investigator to restart his interest in Tertiary molluscan paleontology after an unfortunate hiatus. He is also indebted to Mr. Warren C. Blow for his help with the photographic work.

LOCALITY DATA

The following Tulane University localities are from the Chipola Formation, Calhoun County, Florida:

546. Tenmile Creek, about 1 3/4 miles west of Chipola River (NE 1/4 Sec. 12, T1N, R10W) (=USGS 2212, "one mile west of Bailey's Ferry").

819. Farley Creek, 0.2 mile west of bridge of Florida Highway 275 (SW 1/4 Sec. 21, T1N, R9W).

LITERATURE CITED

DALL, W. H., 1903, Contributions to the Tertiary fauna of Florida: Wagner Free Inst. Sci., Trans., v. 3, no. 6, p. 1219-1654, pls. 48-60.

DREZ, P. E., 1981, Olivinae (Mollusca: Gastropoda) from the Alum Bluff Group of Northwestern Florida: Tulane Stud. Geol. Paleont., v. 16, no. 3, p. 105-122, pls. 1-2.

JUNG, PETER, 1971, Fossil mollusks from Carriacou, West Indies: Bulls. Amer. Paleontology, v. 61, no. 269, 119 p., 21 pls.

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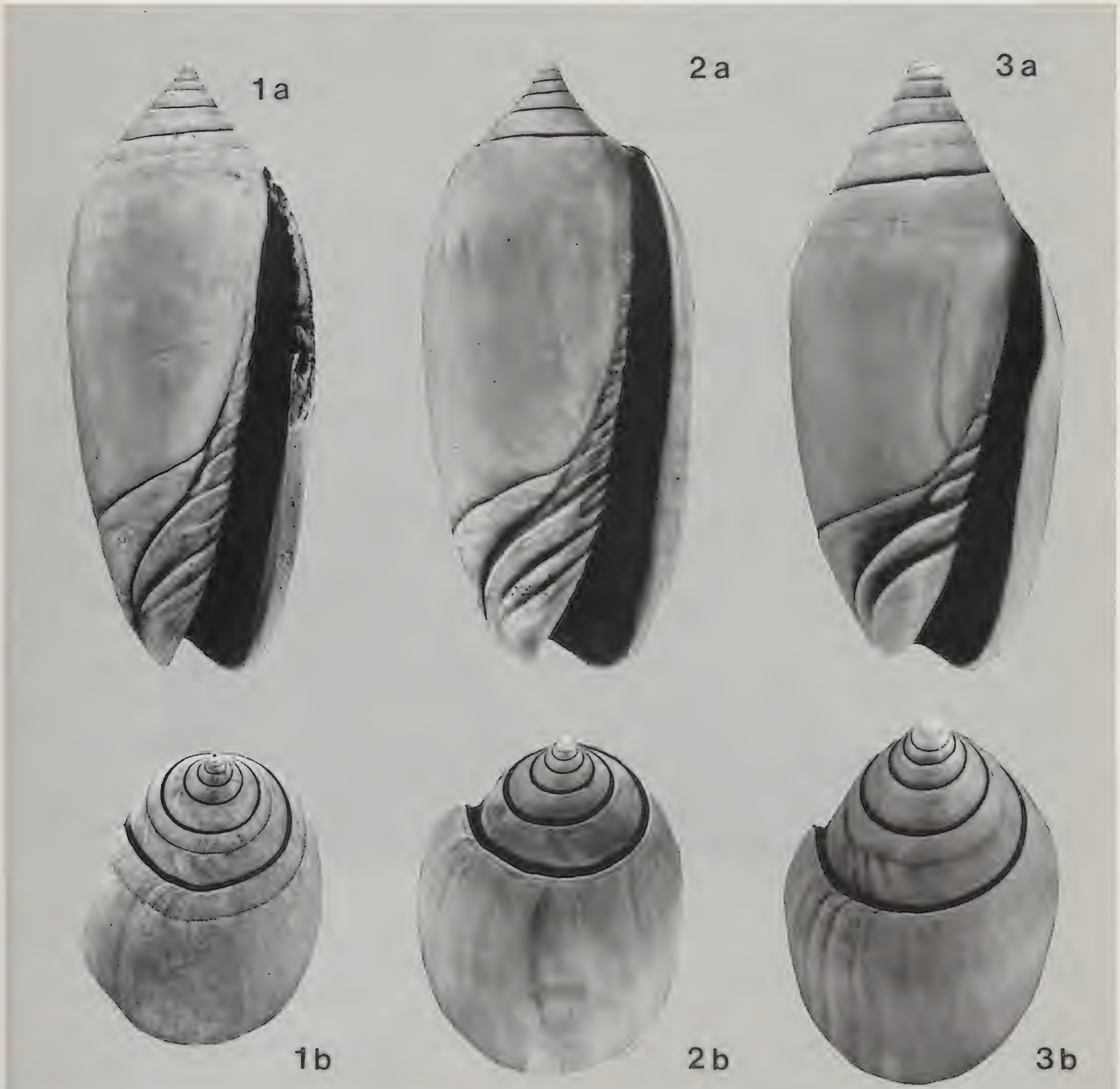

PLATE 1

Figures

1. *Oliva (Omogymna) farleyensis* Drez, n. sp.
   (X 1.5) USNM 496494 (holotype); height 50.6 mm, diameter 21.6 mm.
   Locality: TU 819, Farley Creek, Florida: Chipola Formation.
2. *Oliva (Omogymna) liodes* Dall
   (X2.5) USNM 247895; height 30.5 mm, diameter 13.6 mm.
   Locality: TU 546, Ten Mile Creek, Florida: Chipola Formation.
3. *Oliva (Omogymna) paxillus* Reeve.
   (X3.5) USNM 880194, height 31.7 mm, diameter 10.2 mm.
   Locality: west coast of Mauritius.

VIGNETTES IN COASTAL PLAIN GEOLOGY

HAROLD ERNEST VOKES (1908-)

Harold Vokes was born in Canada but moved with his family to Pasadena, California, when he was 12. There he attended Occidental College, where he originally intended to be an English major, but the usual required Science course in Geology was all that was needed to change his life. A post-doc at Yale led to his appointment at the American Museum in New York, where he was a curator of Invertebrate Paleontology from 1937 to 1943. World War II found him hunting Uranium in the Green River Desert and after the war he joined the faculty at The Johns Hopkins University. Here he began his life-long research on the molluscan faunas of the Gulf and Atlantic Coastal Plain. In 1956, Tulane University, having decided to expand its Geology department and add a graduate program, brought Harold to New Orleans for this purpose. He remained at Tulane for the rest of his professional career, finally retiring from teaching at the then mandatory age of 70, in 1978. However, he continued his research until failing health ended his publishing record in 1994. In the 60 years between 1935 and 1995 Harold published about 130 scientific papers (not including numerous abstracts and book reviews). Undoubtedly, the most valuable contribution was his *Genera of the Bivalvia*, first published in 1967, with a revised edition in 1980, and a final addenda in 1990.

NOTES ON THE FAUNA OF THE CHIPOLA FORMATION – XLIII
ADDITIONS TO THE MOLLUSCAN FAUNA SINCE 1947

EMILY H. VOKES
TULANE UNIVERSITY

In the fifty years since Gardner's monumental study (1926-1947, U.S. Geological Survey Professional Paper 142) of the Alum Bluff molluscan fauna, a large number of species, both new and previously described, have been added to the fauna of the Chipola Formation. These, for the most part, have been published in Tulane Studies in Geology and Paleontology, either in generic monographs or in the series entitled "Notes on the fauna of the Chipola Formation." As a conclusion to this series and to the journal as a whole, a final compilation seems in order.

GASTROPODA

TROCHIDAE

Calliostoma sextoni Schmelz, 1993
Calliostoma cuspidatum Schmelz, 1993

TURBINIDAE

Turbo (Halopsephus?) chipolanus Schmelz, 1995
Turbo (Taeneaturbo) pactilis Schmelz, 1995

MODULIDAE

Modulus(?) imitatus Schmelz, 1991

NERITOPSIDAE

Neritopsis vokesorum R. Hoerle, 1972

CERITHIIDAE

Cerithium louisae Schmelz, 1997
Cerithium (Thericium) peregrinum S. Hoerle, 1972
Cerithium (Thericium) vokesorum S. Hoerle, 1972
Hemicerithium akriton S. Hoerle, 1972
Hemicerithium craticulum S. Hoerle, 1972
Hemicerithium pagodum S. Hoerle, 1972
Tenuicerithium absonum S. Hoerle, 1972
Tenuicerithium ascensum S. Hoerle, 1972
Cerithiopsis inopinus S. Hoerle, 1972
Bittium serenum S. Hoerle, 1972
Alabina (Caloosalba) turbatrix S. Hoerle, 1972

POTAMIDIDAE

Potamides suprasulcatus (Gabb, 1873)
Terebralia dentilabris (Gabb, 1873)

EPITONIIDAE

Cirsotrema (Cirsotremopsis) dalli Rehder, 1945
Scalina gardnerae Olsson, 1967

HIPPONICIDAE

Rothpletzia floridana H. Vokes, 1982

CALYPTRAEIDEA

Calyptraea (Trochita) ornata Basterot, 1825
Calyptraea (Trochita) costaria Grateloup, 1827
Crepipatella apprimus E. Vokes, 1975
Cheilea equestris (Linné, 1758)
Cheilea uncinata (Reeve, 1858)

CYPRAEIDAE

Cypraeorbis emilyae Dolin, 1991
Cypraeorbis hertleini Ingram, 1948 [+ *C. apalachicolae* Ingram, 1948]
Cypraeorbis ballista (Dall, 1915)
Zoila willcoxi (Dall, 1915) [+ *C. alumensis* Ingram, 1948]
Zoila arlettae Dolin, 1991
Trona calhouensis Dolin, 1991
Talparia (Talparia) domininensis (Gabb, 1873)
Talparia (Talparia) mariaelizabethae Dolin, 1991
Mauritia (Mauritia) campbelliana (Pilsbry, 1922)
Lyncina theresae Dolin, 1991
Erronea (Adusta) tumulus (Heilprin, 1886)
Erronea (Adusta) spurcoides (Gabb, 1873)
Erronea (Adusta) shirleyae Dolin, 1991
Bistolida praelatior Dolin, 1991

OVULIDAE

Simnia (Neosimnia) cristata Dolin, 1991
Simnia (Neosimnia) puella Dolin, 1991
Simnia (Spiculata) terminatincta Dolin, 1991
Simnia (Simnialena) oryzagrana Dolin, 1991

TRIVIDAE

Trivia juliae Dolin, 1991
Trivia capillata Dolin, 1991
Dolichupis clypeus Dolin, 1991
Niveria (Niveria) carlottae Dolin, 1991

CASSIDAE

Cassis delta Parker, 1948

TONNIDAE

Eudolium (Galeodolium) subfasciatum Sacco, 1890

CYMATIIDAE

Cymatium (Gutturnium) ritteri Schmelz, 1989

BURSIDAE

Bursa (Bufonariella) chipolana Schmelz, 1997 [for *Bursa (Tutufa) pelouatensis* of Vokes, 1973, not of Cossmann and Peyrot, 1923]

MURICIDAE

Haustellum gilli (Maury, 1910) [= *Murex dasus* Gardner, 1947]
Chicoreus (Chicoreus) dujardinoides (E. Vokes, 1963)
Chicoreus (Chicoreus) lepidotus (E. Vokes, 1963)
Chicoreus (Chicoreus) elusivus E. Vokes, 1974
Chicoreus (Siratus) juliagardnerae E. Vokes, 1970 [n.n. for *Murex gardnerae* Vokes, 1963, non *Alectrion gardnerae* Dall, 1915 = *Chicoreus (Phyllonotus) trophoniformis* (Heilprin, 1887)]
Chicoreus (Siratus) sextoni E. Vokes, 1990
Chicoreus (Phyllonotus) infrequens E. Vokes, 1967
Chicoreus (Phyllonotus) louisae E. Vokes, 1990
Pterynotus (Pterynotus) hoerlei E. Vokes, 1970
Pterynotus (Pterynotus) praepatagiatus E. Vokes, 1992
Poirieria (Panamurex) mauryae E. Vokes, 1970
Dermomurex (Dermomurex) matercula E. Vokes, 1975
Dermomurex (Trialatella) farleyensis E. Vokes, 1975
Dermomurex (Takia) curviductus E. Vokes, 1975
Calotrophon phagon (Gardner, 1947) [originally cited from Oak Grove Fm. only]
Muricopsis (Muricopsis) shirleyae E. Vokes, 1994
Muricopsis (Muricopsis) sp. cf. *praepauxillus* (Maury, 1917)
Muricopsis (Risomurex) crassicosta (Benoist, 1873)
Murexsul nanissimus E. Vokes, 1994
Murexiella (Murexiella) parvula E. Vokes, 1994
Murexiella (Subpterynotus) textilis (Gabb, 1873)
Homalocantha calhounensis (E. Vokes, 1968)
Favartia (Pygmaepterys) drezi (E. Vokes and D'Attilio, 1980)
Urosalpinx xustris Gardner, 1947 [originally cited from Oak Grove Fm. only]
Lindapterys vokesae Petuch, 1987 [for *"Ranella" poppelacki* of Vokes, 1987, not of Hörnes, 1853]
Concholepas drezi E. Vokes, 1972
Typhis (Rugotyphis) keenae Gertman, 1969
Typhis (Typhinellus) chipolanus Gertman, 1969
Pterotyphis (Pterotyphis) calhounensis Gertman, 1969
Pterotyphis (Tripterotyphis) vokesae Gertman, 1969

COLUMBELLIDAE

Parametaria (Parametaria) bella Schmelz, 1995

DOLICHOLATIRIIDAE

Dolicholatirus exilis (Gabb, 1873)

TURBINELLIDAE

Turbinella dodonia (Gardner, 1944) [originally cited from Oak Grove Fm. only]
Turbinella dalli E. Vokes, 1964

VASIDAE

Vasum chipolense E. Vokes, 1966
Vasum haitense (Sowerby, 1850) [Gardner as *Vasum* aff. *engonatum* Dall, 1890, which is a synonym]
Vasum tribulosum E. Vokes, 1970
Vasum elongatum E. Vokes, 1970

VOLUTIDAE

Lyria (Lyria) limata S. Hoerle and E. Vokes, 1978
Falsilyria anoptos S. Hoerle and E. Vokes, 1978

MARGINELLIDAE

Prunum liparum leptochilus Roth, 1973 [n.n. for *Marginella lipara lepta* Gardner, 1938, non Bartsch, 1915]

OLIVIDAE

Oliva (Oliva) waltoniana calhounensis Drez, 1981
Oliva (Oliva?) blowi Drez, 1981
Oliva (Oliva?) vokesorum Drez, 1981
Oliva (Omogymna) farleyensis Drez, 1997
Olivella (Callianax) johnsoni Olsson, 1956

CANCELLARIDAE

Charcolleria distinguenda Petit, 1970
Trigonostoma xiphion Petit and Schmelz, 1991
Trigonostoma serilium Petit and Schmelz, 1991
Trigonostoma nexum Petit and Schmelz, 1991
Trigonostoma ritteri Petit and Schmelz, 1991
Trigonostoma proteus Petit and Schmelz, 1991
Axelella firma Petit and Schmelz, 1991
Axelella axiologa Petit and Schmelz, 1991

CONIDAE

Conus gardnerae S. Hoerle, 1976 [n.n. for *C. corrugatus* Gardner, 1937, non Sowerby, 1870]
Conus aneuretos S. Hoerle, 1976
Conus ambonos S. Hoerle, 1976
Conus cracens S. Hoerle, 1976
Conus tapetus S. Hoerle, 1976
Conus erugatus S. Hoerle, 1976
Conus aquoreus S. Hoerle, 1976
Conus praecipuus S. Hoerle, 1976
Conus vegrandis S. Hoerle, 1976
Conus tricoratus S. Hoerle, 1976
Conus rapunculus S. Hoerle, 1976
Conus sextoni S. Hoerle, 1976

TURRIDAE

Glyphostoma locklini Olsson, 1964

PELECYPODA

MANZANELLIDAE

Nucinella chipolana H. Vokes, 1985

MYTILIDAE

Perna caura H. Vokes, 1986
Musculus (Planimodiola) disinflatus H. Vokes, 1986
Musculus (Ryenella) lateralis praelateralis H. Vokes, 1986
Gregariella arcaforma H. Vokes, 1986
Lithophaga antillarum (d'Orbigny, 1842)
Lithophaga (Diberus) bisulcata (d'Orbigny, 1842)
Modiolus ducatelii Conrad, 1840
Botula fusca (Gmelin, 1791)

PECTINIDAE

Pecten (Pecten) kathrinepalmerae [sic] Tucker, 1930

LIMIDAE

Lima cf. *caribaea* d'Orbigny, 1842
Ctenoides (Ctenoides) floridana (Olsson and Harbison, 1953)
Ctenoides (Ctenoides) cf. *scabra* (Born, 1780)
Limaria (Limaria) chipolana H. Vokes, 1973

OSTREIDAE

Lopha frondicula H. Vokes, 1977

MILTHIDAE

Eomiltha scolaroi H. Vokes, 1969

SPORTELLIDAE

Basterotia (Basterotia) ambona H. Vokes, 1981
Basterotia (Basterotella) miocenica H. Vokes, 1981

ASTARTIDAE

Astarte (Ashtarotha) pansyrta H. Vokes, 1981

CARDIIDAE

Acrosterigma (Vasticardium) hoerleorum H. Vokes, 1977 [for *Cardium inconspicuum* of Gardner, 1926, not of Guppy, 1886]
Trachycardium mollyni H. Vokes, 1982
Trigoniocardia (Trigoniocardia) decidua H. Vokes, 1977
Fragum tunicula H. Vokes, 1977 [for *Cardium aliculum* of Gardner, 1926, not of Dall, 1900]
Papyridea miocica H. Vokes, 1977
Papyridea multicostula H. Vokes, 1977

TELLINIDAE

Arcopagia (Johnsonella) fausta (Pultney, 1799)

DRESSENIDAE

Mytilopsis ermiocenicus H. Vokes, 1985

TRAPEZIIDAE

Coralliophaga deliquiradia H. Vokes, 1989

VENERIDAE

Chione (Chione) oulotricha Gardner, 1936

PETRICOLIDAE

Petricola (Petroxenica) hoerleae H. Vokes, 1976

GASTROCHAENIDAE

Gastrochaena (Spengleria) emilyiana H. Vokes, 1976

HIATELLIDAE

Panopea chipolana H. Vokes, 1985

TEREDINIDAE

Kuphus incrassatus (Gabb, 1873)

CEPHALOPODA

Aturia curvilineata Miller and Thompson, 1937 [Jung has put in synonymy with *A. cubaensis* Lea]

The following is a list of those papers devoted solely to the fauna of the Chipola Formation and/or the Alum Bluff Group. Other species have been described in monographs of various taxa, *e.g., Cenozoic Muricidae of the western Atlantic.*

An Overview of the Chipola Formation, Northwestern Florida
Emily H. Vokes, 1989, v. 22(1): 13-24.

Cerithiidae and Potamididae (Mollusca: Gastropoda) from the Chipola Formation of Northwestern Florida
Shirley E. Hoerle, 1972, v. 10(1): 1-22.

The genus *Conus* (Mollusca:Gastropoda) from the Alum Bluff Group of Northwestern Florida
Shirley E. Hoerle, 1976, v. 12(1): 1-30.

Cardiidae (Mollusca:Bivalvia) from the Chipola Formation, Calhoun County, Florida
Harold E. Vokes, 1977, v. 13(4): 143-189.

Olivinae (Mollusca:Gastropoda) from the Alum Bluff Group of Northwestern Florida
Paul E. Drez, 1981, v. 16(3): 105-122.

Mytilidae (Mollusca:Bivalvia) from the Chipola Formation, Lower Miocene, Florida
Harold E. Vokes, 1986, v. 19(4): 159-174.

Cypraeoidea and Lamellarioidea (Mollusca: Gastropoda), from the Chipola Formation (Late Early Miocene) of Northwestern Florida
Luc Dolin, 1991, v. 24 (1-2): 1-60.

The Genus *Phalium* (Gastropoda:Cassidae) from the Alum Bluff Group of Northwestern Florida
Gary W. Schmelz, 1996, v. 29(2): 45-52.

NOTES ON THE FAUNA OF THE CHIPOLA FORMATION

I. A new species of *Eomiltha* (Mollusca: Bivalvia)
Harold E. Vokes, 1969, v. 7(3): 126-130.

II. *Chicoreus (Siratus) juliagardnerae*, new name for *Murex gardnerae* Vokes *non* Dall, with observations on the species
Emily H. Vokes, 1970, v. 8(2): 51-52.

III. Two new species of *Vasum* (Mollusca: Gastropoda), with comments on *Vasum haitense* (Sowerby)
Emily H. Vokes, 1970, v. 8(2): 88-89.

IV. A new species of *Neritopsis* (Mollusca: Gastropoda)
Robert C. Hoerle, 1972, v. 10(1): 23-24.

V. *Symbiangia*, a new rhizangid coral
John W. Wells, 1972, v. 10(1): 25-27.

VI. On the occurrence of *Pterynotus pinnatus* (Gastropoda:Muricidae) and the problems of dispersal
Emily H. Vokes, 1972, v. 10(1): 29-30.

VII. On the occurrence of the genus *Concho-*

lepas (Gastropoda:Thaididae), with the description of a new species
Emily H. Vokes, 1972, v. 10(1): 31-33.

VIII. On the presence of *Arcopagia (Johnsonella) fausta* (Pulteney) with observations on that species
Harold E. Vokes, 1972, v. 10(1): 34-40.

IX. On the presence of *Kuphus incrassatus* Gabb
Harold E. Vokes, 1972, v. 10(1): 41-46.

X. On the occurrence of the volutid subgenus *Enaeta*
Jean M. Cate, 1972, v. 10(1): 47-50.

XI. Helium-Uranium dating studies of corals
Michael L. Bender, 1972, v. 10(1): 51-52.

XII. Supplementary bibliography
Robert C. Hoerle, 1972, v. 10(1): 53-57.

XIII. The Family Limidae (Mollusca: Bivalvia)
Harold E. Vokes, 1973, v. 10(2): 87-96.

XIV. On the occurrence of *Bursa* (Mollusca: Gastropoda), with comments on the genus
Emily H. Vokes, 1973, v. 10(2): 97-101.

XV. On the occurrence of *"Ranella" poppelacki* Hörnes, a gastropod of uncertain affinities
Emily H. Vokes, 1974, v. 11(2): 96-98.

XVI.On the color pattern of *Globularia fischeri* (Mollusca:Gastropoda)
Emily H. Vokes, 1974, v. 11(2): 99-100.

XVII. On the presence of *Clementia (Ėgesta) grayi* Dall
Harold E. Vokes, 1974, v. 11(2): 101-102.

XVIII. Some new or otherwise interesting members of the Calyptraeidae (Mollusca:Gastropoda)
Emily H. Vokes, 1975, v. 11(3): 163-172.

XIX. On the presence of *Gastrochaena (Splengleria)* (Mollusca:Bivalvia)
Harold E. Vokes, 1976, v. 12(3): 161-162.

XX. A second species of *Petricola (Petricoxenica)* (Mollusca:Bivalvia)
Harold E. Vokes, 1976, v. 12(3): 163-165.

XXI. A new species of the genus *Lopha* (Mollusca:Bivalvia)
Harold E. Vokes, 1977, v. 13(4): 190-191.

XXII. On the occurrence of *Dolicholatirus* (Mollusca:Gastropoda)
Emily H. Vokes, 1977, v. 13(4): 195-198.

XXIII. On the occurrence of the genus *Basterotia* (Mollusca:Bivalvia)
Harold E. Vokes, 1981, v. 16(4): 157-164.

XXIV. The genus *Astarte* (Mollusca: Bivalvia)
Harold E. Vokes, 1981, v. 16(4): 165-167.

XXV. On the occurrence of the genus *Rothpletzia* Simonelli (Mollusca: Gastropoda)
Harold E. Vokes, 1982, v. 17(2): 51-54.

XXVI. A new species of *Trachycardium* from Tenmile Creek
Harold E. Vokes, 1982, v. 17(2): 55-56.

XXVII. On the occurrence of the bivalve genus *Nucella* Wood
Harold E. Vokes, 1985, v. 18(4): 161-163.

XXVIII. On the occurrence of the non-marine genus *Mytilopsis* (Mollusca: Bivalvia)
Harold E. Vokes, 1985, v. 18(4): 163-165.

XXIX. A new species of *Panopea* (Mollusca: Bivalvia)
Harold E. Vokes, 1985, v. 18(4): 165-168.

XXX. On the presence of *Eudolium (Galeodolium) subfasciatum* Sacco (Gastropoda:Tonnidae)
Emily H. Vokes, 1986, v. 19(4): 177-180.

XXXI. On the occurrence of the genus *Coralliophaga* (Mollusca:Bivalvia)
Harold E. Vokes, 1989, v. 22(4): 127-130.

XXXII. A new species of the genus *Cymatium* (Mollusca:Gastropoda)
Gary W. Schmelz, 1989, v. 22(4): 137-139.

XXXIII. Variations on a theme – the color pattern in *Smaragdia chipolana* (Gastropoda:Neritidae)
Emily H. Vokes, 1990, v. 23(4): 130-131.

XXXIV. New species of Cancellarioidea (Mollusca:Gastropoda)

Richard E. Petit and Gary W. Schmelz, 1991, v. 24(3): 61-69.

XXXV. A new species of the genus *Modulus* (Mollusca:Gastropoda)
Gary W. Schmelz, 1991, v. 24(4): 101-103.

XXXVI. Two new species of the genus *Calliostoma* (Gastropoda:Trochidae)
Gary W. Schmelz, 1993, v. 26(1): 41-45.

XXXVII. Variation in the shell morphology of *Calliostoma ceramicum* (Gastropoda: Trochidae)
Gary W. Schmelz, 1993, v. 26(1): 46-47.

XXXVIII. Two new species of the genus *Turbo* (Gastropoda:Turbinidae)
Gary W. Schmelz, 1995, v. 28(4): 113-115.

XXXIX. A new species of the genus *Parametaria* (Gastropoda:Columbellidae)
Gary W. Schmelz, 1995, v. 28(4): 116-118.

XL. A new species of the genus *Cerithium* (Mollusca:Gastropoda)
Gary W. Schmelz, 1997, v. 29(4): 153-155.

XLI. A reexamination of *Bursa* (Mollusca: Gastropoda) from the Chipola Formation, with the description of a new species
Gary Schmelz, 1997, v. 30(2): 105-108.

XLII. A new species of *Oliva (Omygymna)* (Gastropoda: Olividae)
Paul E. DRrez, 1997, v. 30(3): 187-189

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VIGNETTES IN COASTAL PLAIN GEOLOGY

EMILY HOSKINS VOKES

(1930-)

Although born in northern Louisiana, Emily Hoskins moved to New Orleans at a young age. Working as a laboratory technician (in Biophysics) at Tulane University, she availed herself of the opportunity to take courses in Geology, with the ultimate goal of becoming a geomorphologist. This goal changed suddenly after meeting paleontologist Harold Vokes, who came to Tulane in 1956 to become Chairman of the Geology Department. She began her lifelong interest in the Muricidae as a graduate student and ultimately published some 150 papers, primarily on this group but also on a variety of other Cenozoic Gastropoda. Her entire professional career was spent at Tulane University, where she began as an Instructor in Geography in 1969, including ten years as Chairman of the Geology Department and one year as Acting Dean of Newcomb College. She became Associate Editor of *Tulane Studies in Geology and Paleontology* in 1970, and Co-Editor in 1986.

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